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A NEW *SEPIELLA* GRAY, 1849 (CEPHALOPODA: SEPIIDAE) FROM NORTHERN AUSTRALIA, WITH A REDESCRIPTION OF *SEPIELLA WEBERI* ADAM, 1939

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ABSTRACT

Examination of specimens of *Sepiella Gray*, 1849, from northern Australia led to the discovery of a second species in addition to *Sepiella weberi* Adam, 1939, already known to occur in the region. This species is described here as *Sepiella mangkangunga* sp. nov., and *Sepiella weberi* is redescribed from the types and Australian material. The two species, while occupying a narrow geographic range, were collected at different depths. *Sepiella weberi* is found between 77–88 m in Australian waters (though the type specimens from Indonesia were collected at 18 m, and at the surface), and *S. mangkangunga* sp. nov. occurs in shallow water, between 1.1 and 3.3 m.

KEYWORDS: Cephalopoda, Sepiidae, *Sepiella mangkangunga* sp. nov., *Sepiella weberi*, northern Australia

INTRODUCTION

The genus *Sepiella* was erected by Gray (1849) for cuttlefish with numerous, similar sized suckers in 8–10 rows on the tentacular clubs, and with an oblong cuttlebone, convex ventrally, the posterior end of which is expanded and chitinous. The name subsequently sank into obscurity until Steenstrup (1880) later redefined the group, thus reinstating its importance (Lu 1998). Khromov *et al.* (1998) define the genus by the presence of a gland and gland pore at the posterior end of the mantle between the fins, and in having a triangular tubercle on the mantle locking cartilage which corresponds to a depression in the funnel locking cartilage. The inner cone of the sepion has very short limbs.

Khromov *et al.* (1998) recognise six species in the genus: *Sepiella cyanea* Robson, 1924; *S. inermis* d'Orbigny, 1848; *S. japonica* Sasaki, 1929; *S. ocellata* Pfeffer, 1884; *S. ornata* (Rang, 1837), and *S. weberi* Adam, 1939. The status of *S. ocellata* is described as questionable; this species is possibly a synonym of *S. ornata* (Khromov *et al.* 1998). *Sepiella weberi* was the only species known from Australian waters, reported from near Darwin, 12°27'S 130°50'E (Lu 1998). It was originally described from two eastern Indonesian specimens: a male from Timor, near Koepang, 8°35'S 126°00'E, and a female from Soemba, 10°S 119°56'E. Iredale (1954) described a second species, *S. melwardi*, based on cuttlebones collected from Melville Island, Australia, 11°35'S 131°10'E. Lu (1998) placed *S. melwardi* in synonomy with *S. weberi*.

Members of this genus occur only off southern Africa, the Red Sea and the Indo-West Pacific. All species are found in relatively shallow water, with the deepest occurrence at approximately 150 m. Adam's (1939) revision of the group is the most recent detailed work on the genus. While Adam (1939) clarified the status of a number of species, it is likely that as representatives of the genus can be quite similar morphologically, a number of cryptic species may remain to be discovered.

Recent examination of all *Sepiella* material housed in the Museum of Victoria

collection led to the discovery of a new species from northern Australia. This species, the second now known to occur in Australian waters, does not conform to any of the above listed nominal species, differing in a number of characters, primarily of the cuttlebone and tentacular club. A full description of the new species is presented in this paper, with a redescription of *S. weberi*. The two species, while occupying a narrow geographic range, were collected at different depths in Australian waters. *Sepiella weberi* has been reported from between 77 and 88 m off northwestern Australia. Adam's (1939) type specimen from Soemba was collected at 18.3 m, and a second, from Timor, was collected at the surface using an electric light. *Sepiella mangkangunga* sp. nov. from Australia occurs in shallow water between 1.1 and 3.3 m.

MATERIALS AND METHODS

This work was based on museum material. All material studied is listed in the Material examined sections given with each species description. Institutional acronyms used throughout the paper are: AM – Australian Museum, Sydney, Australia; MV – Museum Victoria, Melbourne, Australia; NTM – Museum and Art Gallery of the Northern Territory; ZMA – Zoologisch Museum, Universiteit van Amsterdam. Other abbreviations: coll. – collected, F – female, FV – Fisheries Vessel, Is. – Island, J – juvenile, m – metres, M – male, mm – millimetres, RV – Research Vessel.

Measurements and indices used throughout this paper are primarily those given in Roper and Voss (1983), using dorsal mantle length (ML) as a size standard. Some additional measurements are used, and these with the definitions listed by Roper and Voss (1983) are given in Table 1. Parts of the club and arm sucker rims are described using the terminology of Nixon and Dilly (1977), and nomenclature for radulae follows Nixon (1995). Beaks were described following Clarke (1986). Diagrammatic illustrations of measurements and terminology used for particular structures are shown in Fig. 1.

Measurements were made either using dial callipers, or an eyepiece micrometer attached to a stereo microscope. All measurements are expressed in millimetres (mm). Measurements and counts for individual specimens are shown in tables accompanying descriptions. Ranges of arm length indices, arm sucker diameter indices, and arm sucker counts are also presented in tables accompanying descriptions. Ranges for all other characters appear in the text. In species descriptions and tables, the range of values for each character are expressed as: minimum – mean – maximum [standard deviation (SD)]. Values for each sex are given separately. Numbers shown in bold with the range of measurements for mantle length indicate the upper size limit for each sex (numbers appear after the upper limit of the range when the largest specimens were not necessarily among the specimens selected for detailed examination and measurement for all characters).

Measurements for structures which were clearly distorted or broken were not attempted, and these, in addition to missing values, appear as a dash (–) in the tables. Ranges for specific character traits given with each species description do not, therefore, always refer to the total number of specimens examined for each species. Measurements for *S. weberi* Adam syntypes are included in Table 4, but are not included in the ranges of indices included with species descriptions.

For scanning electron microscopy, arm and club suckers were removed from the middle of designated arms and the tentacular club, and dehydrated in an ethanol series through to 100% ethanol then air dried. Radulae and beaks were dissected from the buccal mass, and soaked for approximately half an hour in a warm, saturated potassium hydroxide solution, then radulae were cleaned using forceps and a fine brush. In all cases, the new unused portion of the radula was examined. All prepared material was mounted, gold coated and examined in a JSM 6400 (Japan Electron Optics Ltd. Japan) scanning electron microscope operated at 15 kV.

Table 1. Description of measurements and counts. Definitions largely follow Roper and Voss (1983). New or modified definitions are indicated by an asterisk (*). Indices (shown in square brackets) are calculated by dividing each measure by mantle length or, for cuttlebone characters, cuttlebone length (unless otherwise specified).

Arm Length – **AL**: length of each designated (i.e. 1, 2 etc.) arm measured from first basal (proximal-most) sucker to distal tip of arm (Arm 1, dorsal; 2, dorso-lateral; 3, ventro-lateral; 4, ventral) [**ALI**].

Anterior Mantle to Head length * – **AMH**: dorsal length of mantle measured from anterior-most point of mantle to intersection of transverse line joining dorso-lateral mantle margin [**AMHI**].

Arm Sucker Count * – **ASC**: total number of suckers on each designated arm (e.g. ASC2).

Arm Sucker diameter – **AS**: diameter of largest sucker on each designated (i.e. 1, 2 etc.) arm [**ASIn**]. Suckers on left ventral hectocotylised arms are differentiated as follows:

Arm Sucker left 4 * – **ASl4**: diameter of largest sucker on left ventral arm of male [**ASInl4**].

Arm Sucker left 4 minimum * – **ASl4m**: diameter of smallest arm sucker on hectocotylised portion of left ventral arm of male [**ASInl4m**].

Cuttlebone Breadth – **CbB**: greatest dorso-ventral breadth of cuttlebone [**CbBI**].

Cuttlebone Length – **CbL**: dorsal length of cuttlebone along midline.

Cuttlebone Width – **CbW**: greatest width (perpendicular to longitudinal axis) of cuttlebone [**CbWI**].

Club Length – **ClL**: length of tentacular club measured from proximal-most basal suckers (carpus) to distal tip of club [**ClLI**].

Club Row Count – **ClRC**: number of suckers in transverse rows (dashed line in Fig. 1) on tentacular club.

Club Sucker diameter – **ClS**: diameter of largest sucker on tentacular club [**ClSI**].

Club Sucker dorsal * – **ClSd**: diameter of largest tentacular club sucker in dorsal-most (closest to swimming keel) longitudinal row [**ClSId**].

Club Sucker ventral * – **ClSv**: diameter of largest tentacular club sucker in ventral-most (opposite swimming keel) longitudinal row [**ClSIv**].

Eye Diameter – **ED**: diameter of eye [**EDI**].

Egg Diameter * – **EgD**: diameter of egg [**EgDI**].

Free Funnel length – **FFu**: the length of the funnel from the anterior funnel opening to the point of its dorsal attachment to the head [**FFuI**].

Fin Insertion anterior * – **FIa**: anterior origin of fin measured from mantle margin to anterior-most junction of fin and mantle [**FIIa**].

Fin Insertion posterior* – **FIp**: measured between posterior junctions of fins with mantle [**FIIp**].

Funnel Length – **FuL**: the length of the funnel from the anterior funnel opening to the posterior margin measured along the ventral midline [**FuLI**].

Fin Width – FW: greatest width of single fin [**FWI**].

Gill Lamellae Count – **GiLC**: number of lamellae on outer demibranch including the terminal lamella.

Gill Length * – **GiL**: length of gill [**GiLI**].

Head Length – **HL**: dorsal length of head measured from point of fusion of dorsal arms to anterior tip of nuchal cartilage [**HLI**].

Head Width – **HW**: greatest width of head at level of eyes [**HWI**].

Loculus Length * – **LoL**: length of the last loculus (ventral anterior smooth zone of the cuttlebone) [**LoLI**].

Mantle Length – **ML**: dorsal mantle length. Measured from anterior-most point of mantle to posterior apex of mantle.

Mantle Width – **MW**: greatest straight-line ventral width of mantle [**MWI**].

Spermatophore Length – **SpL**: length of spermatophore [**SpLI**].

Spermatophore Width – **SpW**: greatest width of spermatophore. Spermatophore width index is expressed as a percentage of spermatophore length [**SpWI**].

Striated Zone length – **StZ**: length of striated zone of cuttlebone [**StZI**].

Transverse Row Count – **TrRC**: number of suckers in longitudinal series on tentacular club (counted from proximal-most basal suckers (carpus) to distal tip of club).

Ventral Mantle Length – **VML**: length of ventral mantle measured from anterior mantle margin at ventral midline, to posterior apex of mantle [**VMLI**].

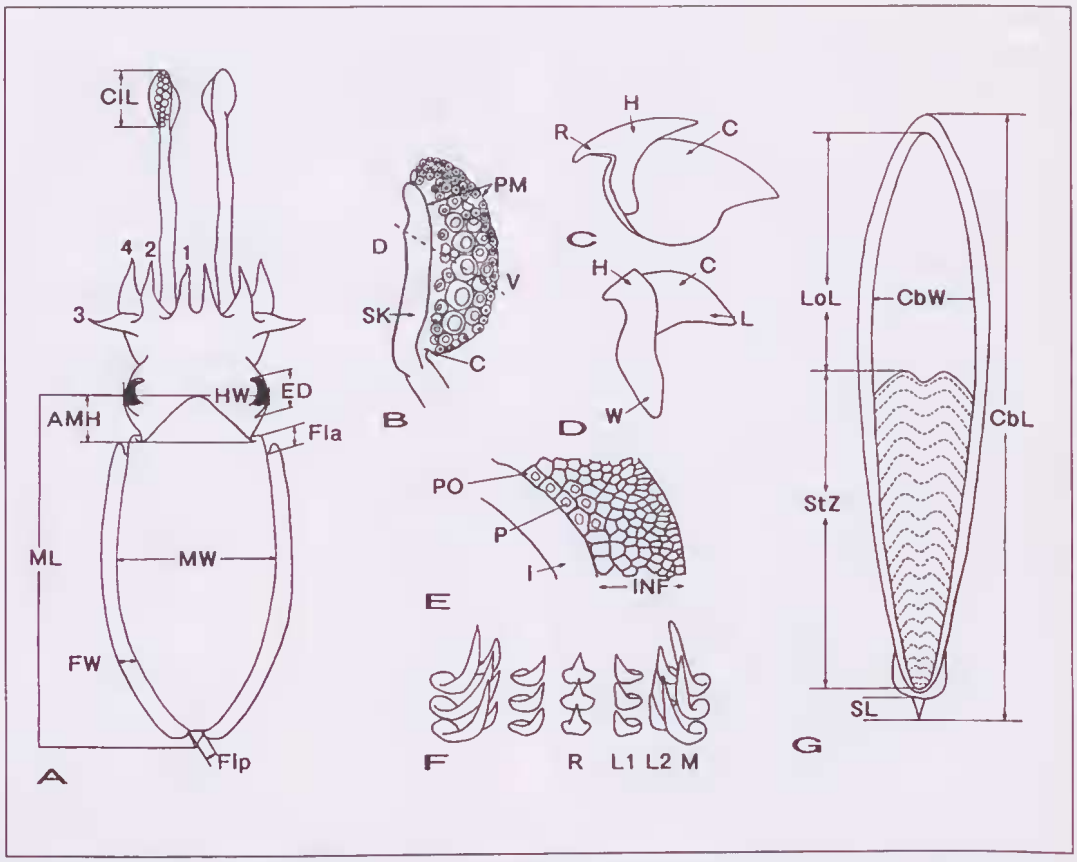

Fig. 1. Measurements and terminology. **A**, whole animal dorsal view (for abbreviations and definitions see Table 1); **B**, tentacular club (C – carpus, D – dorsal, PM – protective membranes, SK – swimming keel, V– ventral). The number of suckers intersected in an oblique transverse line across the club, shown as a hatched line on this figure, is the Club Row Count (ClRC). In the example illustrated ClRC = 4.; **C**, upper beak (C – crest, H – hood, R – rostrum); **D**, lower beak (C – crest, H – hood, L – lateral wall, W – wing); **E**, arm sucker rim (I – inner ring, INF – infundibulum, PO – polygonal process, P – peg); **F**, radula (R – rhachidian teeth, L1 – first lateral teeth, L2 – second lateral teeth, M – marginal teeth); **G**, cuttlebone, ventral view (for abbreviations and definitions, see Table 1). (A and G modified from Roper and Voss 1983: figure 1).

Species descriptions were generated by the DELTA (DEscription Language for TAxonomy) system (Dallwitz 1980; Dallwitz *et al.* 1993; Partridge *et al.* 1993).

The statistics package 'Systat' (Systat Incorporated) was used to examine sexual dimorphism in morphometric characters for *Sepiella mangkangunga* sp. nov. Slopes and intercepts of regression equations were compared statistically between sexes for those characters showing a significant correlation with body size. For soft parts, mantle length was used as a size indicator. For cuttlebone characters, cuttlebone length was used. An insufficient number of male specimens available for study precluded similar comparisons between sexes being made for *Sepiella weberi*.

SYSTEMATICS

Sepiella mangkangunga sp. nov.
(Figs 1-11; Tables 1-6)

Sepiella melwardi Iredale, 1954: 78–79 (in part), plate V, figs 4–6.

Type material. HOLOTYPE – NTM P10606, Australia: Northern Territory, off Stingray Head – M (42.0 mm ML), 12°48'S

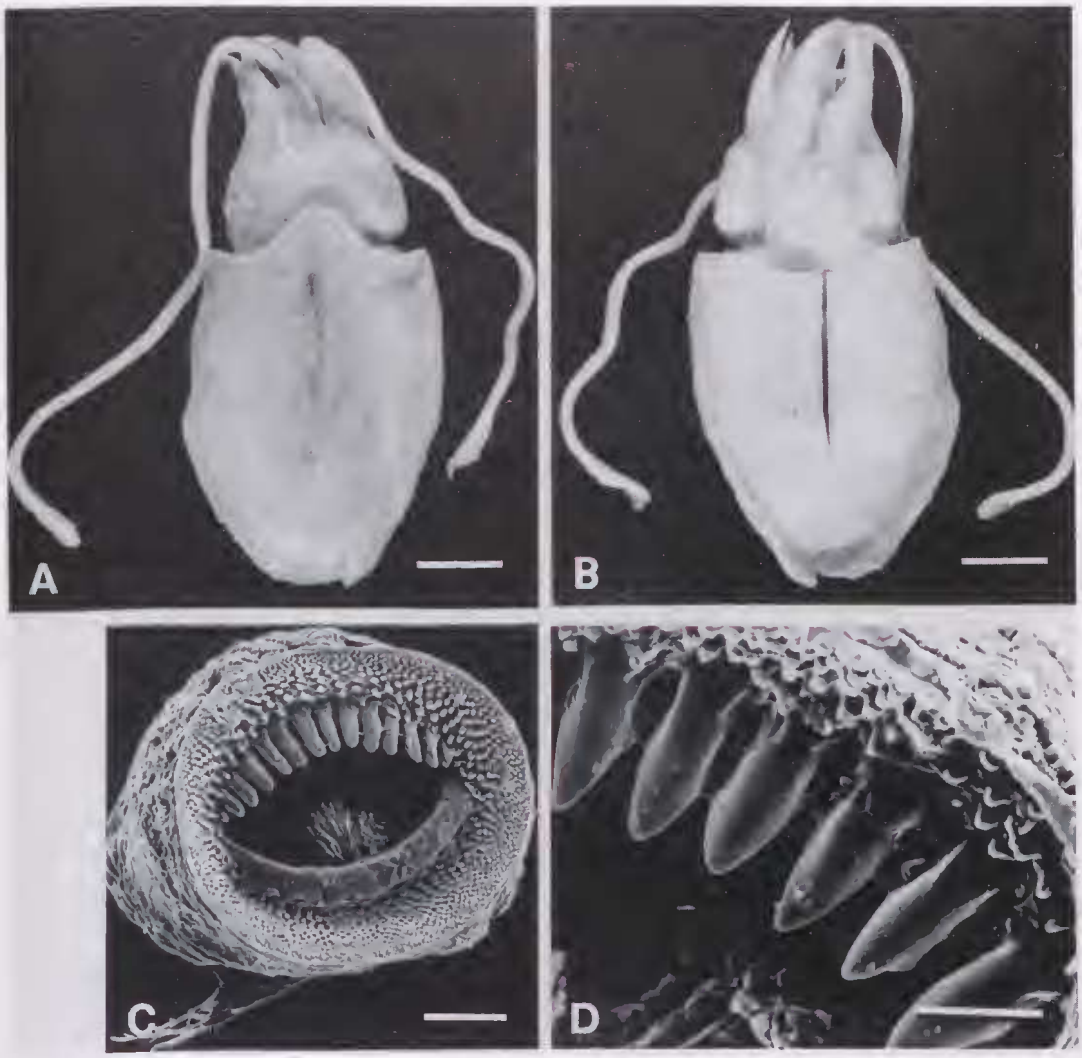

Fig. 2. *Sepiella mangkangunga* sp. nov. **A**, dorsal view, male, MV F65573, 41.5 mm ML, scale bar 10 mm; **B**, ventral view, same specimen; **C**, sucker, arm 2, male, NTM P11116, 34.0 mm ML, scale bar 100 µm; **D**, enlargement of sucker rim arm 2, male, NTM P11116, 48.1 mm ML, scale bar 30 µm.

130°21'E, 2.3-2.1 m, 5 June 1987, coll. N. Gill, N.T. Fisheries. PARATYPES – (NTM P16082), Australia: Northern Territory, off Stingray Head – 2M (45.7, 38.0 mm ML), 2F (43.2, 52.2 mm ML), 12°48'S 130°21'E, 2.3-2.1 m, 5 June 1987, coll. N. Gill, N.T. Fisheries; (MV F80992), collection data as for NTM P16082 – 3M (38.6-45.8 mm ML) 3F (45.2-34.7 mm ML).

Additional material. Australia: Northern Territory – 1 cuttlebone (44.0 mm CbL), Melville Is., Condon Bay, 11°35'S 131°10'E, on beach, coll. M. Ward, (AM C133321); 14M (23.1–52.5 mm ML) 12F (24.6–57.8 mm ML) 16J (16.3–26.5 mm ML), off Stingray Head, 12°48'S 130°21'E, 2.1–1.2 m, 18 August 1987, coll. N. Gill on FV *John Lake*, (MV F65574); 10M (24.8 –57.6 mm ML) 7F (23.7–57.2 mm ML) 2J (17.6, 21.2 mm ML), 2.8–1.1 m, 3 September 1987, coll. N. Gill on FV *John Lake*, (NTM P11116); 19M (32.2–50.5 mm ML) 7F (34.8–55.0 mm ML) 31J (16.1–35.0 mm ML), 2.6–1.6 m, 4 June 1987, coll. N. Gill, N.T. Fisheries, (MV F65572); 5M (37.7–41.5 mm ML) 8F (39.1–48.0 mm ML)

45J (18.2–34.9 mm ML), 2.3–2.1 m, 5 June 1987, coll. N. Gill, N.T. Fisheries, (MV F65573); 7F (36.1–54.0 mm ML) 7J (14.7–31.1 mm ML), mouth of Finniss River, 12°53'S 130°32'E, 3.3–2.5 m, 4 June 1987, coll. N. Gill, N.T. Fisheries, (MV F65569); 2M (28.7, 32.9 mm ML) 9F (24.0–58.5) 2J (19.3, 30.8 mm ML), Finniss River Channel, 12°53'S 130°32'E, 2.9–1.5 m, 5 June 1987, coll. N. Gill, N.T. Fisheries, (NTM P11117); 3M (33.3–40.1 mm ML) 3F (32.3–50.6 mm ML), Little Finniss River, 13°14'S 130°57'E, 1.2 m, 4 June 1987, coll. N.T. Fisheries, (MV F65576).

Diagnosis. Club with 12–15 suckers in transverse rows; swimming keel shorter than carpus. Dorsal mantle without ovoid markings at base of fins. Cuttlebone strongly convex in lateral view; posterio-lateral margin of outer cone with pronounced indentation.

Description. Counts and indices for individual specimens are given in Tables 2–3; ranges for arm length indices, arm sucker diameter indices and arm sucker counts are shown in Table 4.

Small to moderate sized species; ML males 38.0–45.1–**57.6** (SD, 6.5), females 43.2–53.4–57.7, **58.5** (SD, 4.6). Mantle oval; MWI males 45.7–57.5–67.4 (SD, 8.4), females 49.1–55.5–68.2 (SD, 7.0); dorsal anterior margin triangular, obtuse (Fig. 2A); extending anteriorly to level of middle of eyes; AMHI males 9.7–11.9–13.8 (SD, 1.5), females 8.0–10.9–13.0 (SD, 1.6). Ventral mantle margin emarginate, without distinct lateral angle (Fig. 2B); VML1 males 66.0–78.3–84.1 (SD, 5.1), females 75.8–80.9–85.9 (SD, 3.6). Fins widest in posterior third; FWI males 15.7–18.3–20.0 (SD, 1.3), females 16.7–19.0–21.3 (SD, 1.8); anterior origin posterior to mantle margin; FIIa males 6.0–11.0–15.8 (SD, 3.3), females 4.7–9.4–14.4 (SD, 3.6); ending in lobes which lie very close together; narrow gap between fins; FIIp males 2.4–3.3–4.1 (SD, 0.7), females 1.6–2.2–2.9 (SD, 0.5). Funnel long, broad-based; extends to interbrachial area of ventral arms (Fig. 2B); FuLI males 25.7–35.2–42.2 (SD, 5.2), females 28.3–33.9–40.2 (SD, 4.2). Funnel free portion approximately half funnel length; FFuI males 10.4–14.9–20.4 (SD, 3.2), females 11.0–15.5–20.5 (SD, 2.8). Funnel organ dorsal elements inverted V-shape with small papilla in front; ventral elements oval (Fig. 3A). Mantle-locking cartilage curved, with triangular tubercle; funnel-locking cartilage with depression which corresponds to tubercle (Fig. 3B). Head short; HLI males 27.6–33.6–38.1 (SD, 3.5), females 28–33.8–41.2 (SD, 4.6); broad, narrower than mantle; HWI males 43.7–47.9–53.2 (SD, 2.9), females 40.1–47.5–52.6 (SD, 4.8). Eyes moderate size; EDI males 13.0–15.5–19.5 (SD, 1.9), females 13.0–15.8–17.6 (SD, 1.6); ventral eyelids present.

Male and female arms subequal in length (Table 4). Arm length index of longest arms in males (ALI4) 50.4–60.5–73.5 (SD, 7.3), females (ALI4) 34.7–44.3–57.5 (SD, 8.9). Protective membranes in both sexes narrow; normal, not thickened. Distal arm tips in both sexes strongly attenuate, suckers enclosed by protective membranes. Arm suckers tetrastrial in both sexes. Two median series of suckers larger than dorsal and ventral marginal series in males; larger than female arm suckers (Fig. 11, Tables 4–5). Chitinous rims of arm suckers with marked sexual dimorphism. In males, distal margin of inner ring with 14-16 elongate tooth-like processes (Fig. 2C–D), proximal margin smooth; in females, distal half of inner ring with two to three rows of tooth-like structures, inner ring proximal margin with blunt projections (Fig. 4A); infundibulum in both sexes with 11–15 rows of hexagonal processes with pegs on innermost rows, outer processes without pegs (Figs 2C, 4A). In males, infundibular processes on inner margin of toothed side of ring narrow, elongate (Fig. 2C–D). Sucker counts range from 60–130; females with higher average counts than males (Table 4).

Hectocotylus present in males, left ventral arm modified; sucker size reduced proximally, eight to nine rows of reduced suckers; suckers in two dorsal series smaller than remaining suckers (Fig. 3C); two dorsal series widely spaced, suckers markedly reduced; two ventral series close together, suckers alternate; maximum and minimum sucker diameters: ASInl4 2.47–2.69–2.98 (SD, 0.13), ASInl4m 0.30–0.55–0.71 (SD, 0.12). Oral surface of

Table 2. Measurements (mm), counts and indices of 10 male *Sepiella mangkangunga* sp. nov.

Museum Reg. No.	NTM P16082 (Paratype)	MV F80992 (Paratype)	MV F80992 (Paratype)	MV F65573	NTM P10606 (Holotype)	NTM P16082 (Paratype)	MV F80992 (Paratype)	MV F65574	MV F65574	NTM P11116
Maturity	immature	immature	immature	immature	mature	mature	mature	mature	mature	mature
ML	38.0	38.6	39.3	41.5	42.0	45.7	45.8	49.6	52.5	57.6
AMHI	11.6	11.4	13.7	13.3	13.8	9.8	11.6	13.1	9.7	11.1
VMLI	81.8	77.2	76.1	66.0	78.8	76.8	84.1	80.0	83.4	79.2
MWI	62.4	65.3	67.4	65.8	61.4	55.4	57.4	47.6	45.7	46.2
FWI	18.4	17.4	18.1	15.7	17.4	18.2	18.8	19.0	20.0	19.8
AFII	15.8	12.2	11.5	14.5	11.9	9.8	13.8	6.0	8.4	6.3
PFII	3.9	3.1	2.5	4.1	2.4	3.5	3.3	-	-	-
FuLI	42.1	38.9	33.1	42.2	32.1	37.2	37.1	32.3	25.7	31.3
FFuI	15.8	16.8	20.4	12.0	16.7	17.5	15.3	12.1	11.6	10.4
HLI	37.9	35.0	34.4	38.1	35.7	27.8	33.6	32.5	32.8	27.6
HWI	53.2	47.9	47.1	47.7	46.2	45.5	43.7	49.6	51.8	46.7
EDI	19.5	14.8	15.3	13.3	14.3	16.8	15.5	15.5	16.8	13.0
AL1I	43.4	46.6	44.5	62.7	53.6	48.1	54.6	40.3	43.8	36.5
AL2I	52.6	47.9	44.5	50.6	56.0	48.1	54.6	46.4	47.6	39.9
AL3I	52.6	49.2	53.4	62.7	61.9	55.8	65.5	52.4	53.3	46.9
AL4rI	60.5	62.2	56.0	73.5	64.3	56.9	67.7	50.4	53.3	-
AL4lI	60.5	62.2	58.5	66.3	64.3	52.5	72.1	54.4	57.1	53.8
AS1In	2.29	3.24	2.54	3.25	2.98	2.89	2.73	2.62	2.99	2.52
AS2In	2.50	2.90	2.54	2.89	2.98	2.74	2.62	2.52	2.99	2.60
AS3In	2.37	2.59	2.42	2.70	3.10	2.74	2.62	2.62	2.70	2.52
AS4rIn	2.63	2.85	2.54	2.58	2.55	2.74	2.73	2.62	2.70	2.08
ASC1	60	66	74	70	75	72	74	64	76	65
ASC2	64	76	72	74	76	74	78	69	82	68
ASC3	84	90	96	98	94	84	88	82	94	90
ASC4	78	90	85	90	88	94	92	84	86	80
AS4llIn	2.63	2.59	2.47	2.65	2.98	2.74	2.73	2.76	2.70	2.60
AS4lmIn	0.18	0.18	0.18	0.17	0.17	0.22	0.15	0.14	0.29	-
C1LI	34.2	46.6	38.2	37.3	40.5	35.0	32.8	-	-	36.5
C1RC	12	12	14	12	12	14	14	-	-	15
TrRC	50	60	52	42	45	55	43	-	-	52
C1SI	0.58	0.65	0.64	0.60	0.60	0.55	0.55	-	-	0.69
C1SdI	0.45	0.57	0.43	0.53	0.48	0.48	0.55	-	-	0.61
C1SvI	0.45	0.52	0.51	0.48	0.48	0.55	0.55	-	-	0.64
GiLC	25	25	26	-	-	25	26	26	25	26
GiLI	36.8	36.8	36.4	31.6	41.9	34.8	37.3	25.0	26.9	26.2
SpLI	-	-	-	-	7.8	7.6	8.5	8.5	8.6	8.7
SpWI	-	-	-	-	0.24	0.26	0.26	0.24	0.23	0.26
CbL	36.0	36.8	36.5	39.9	42.4	44.3	47.0	47.0	47.7	-
CbWI	30.6	30.7	30.7	32.1	33.0	30.2	27.4	29.1	31.4	-
CbBI	15.3	15.5	15.1	15.0	14.4	15.8	14.5	11.9	14.5	-
StZI	48.6	48.9	54.8	50.1	50.8	54.2	49.7	55.3	56.0	-
LoLI	40.3	38.0	38.4	40.1	40.6	37.7	38.4	31.9	28.5	-
LoL/Stz(%)	82.9	77.8	70.0	80.0	80.0	69.6	77.3	57.7	50.9	-

Table 3. Measurements (mm), counts and indices of 10 female *Sepiella mangkangunga* sp. nov.

Museum Reg. No.	NTM P16082 (Paratype)	MV F65574	MV F80992 (Paratype)	NTM P16082 (Paratype)	NTM P11116	MV F80992 (Paratype)	MV F65574	NTM P11116	NTM P11117	MV F65574
Maturity	immature	immature	immature	immature	mature	mature	mature	mature	mature	mature
ML	43.2	48.9	51.2	52.2	54.6	54.7	56.8	57.2	57.4	57.7
AMHl	13.0	12.1	12.3	9.0	9.7	11.2	10.2	8.0	10.6	12.5
VMLl	75.9	83.2	75.8	78.9	85.9	77.5	84.9	83.2	81.7	81.6
MWl	66.7	49.1	58.2	68.2	52.7	55.0	51.8	49.1	54.7	49.2
FWl	16.7	19.0	21.3	17.2	20.0	21.0	21.0	18.7	17.2	18.2
AFIl	12.0	4.7	12.5	12.8	5.5	14.4	8.1	5.8	11.5	6.8
PFIl	1.6	-	2.0	2.9	-	2.4	-	-	-	-
FuLl	39.4	30.7	28.3	40.2	34.8	36.6	29.9	33.2	36.6	29.5
FFul	18.5	14.3	20.5	15.3	11.0	17.4	15.8	13.1	14.8	13.9
HLl	38.0	29.7	41.2	37.4	32.4	35.6	28.2	28.1	37.1	30.3
HWl	50.0	52.1	41.0	47.5	52.6	41.7	50.2	50.9	40.1	49.0
EDl	16.4	16.2	13.9	16.1	13.0	16.8	17.6	14.3	16.2	17.5
AL1l	38.2	28.6	46.9	45.0	36.6	40.2	33.5	29.7	48.8	31.2
AL2l	41.7	34.8	46.9	47.9	39.4	40.2	29.9	33.2	48.8	34.7
AL3l	44.0	36.8	50.8	46.0	38.5	42.0	33.5	36.7	50.5	34.7
AL4l	52.1	34.8	52.7	52.7	38.5	46.6	38.7	35.0	57.5	34.7
AS1ln	1.62	0.92	1.56	1.53	1.59	1.37	1.76	1.75	1.34	2.08
AS2ln	1.74	1.23	1.46	1.53	1.74	1.59	1.76	1.84	1.31	1.73
AS3ln	1.74	1.57	1.56	1.48	1.59	1.59	1.62	1.75	1.31	1.39
AS4ln	1.44	1.43	1.46	1.44	1.83	1.37	1.76	1.84	1.39	1.73
ASC1	88	108	100	96	98	96	-	98	94	102
ASC2	98	112	116	120	-	98	-	114	110	104
ASC3	112	118	130	120	-	104	-	120	120	108
ASC4	90	114	126	118	100	110	112	108	106	100
C1LI	41.7	-	41.0	38.3	45.8	35.6	37.0	-	34.8	-
C1RC	14	-	15	14	15	15	15	-	15	-
TrRC	50	-	50	54	52	48	54	-	54	-
C1SI	0.58	-	0.49	0.48	0.77	0.46	0.70	-	0.44	-
C1SdI	0.46	-	0.39	0.38	0.59	0.46	0.48	-	0.44	-
C1SvI	0.46	-	0.39	0.42	0.73	0.46	0.79	-	0.44	-
GiLC	26	28	26	26	28	25	30	28	28	30
GiLI	39.6	31.5	35.9	46.2	27.5	37.5	29.6	26.9	37.6	22.2
EgLI	-	-	-	-	5.2	-	3.9	4.5	2.8	4.7
CbL	42.7	46.0	50.5	49.6	-	49.4	57.0	55.0	54.4	55.0
CbWl	23.2	33.5	30.7	33.1	-	33.4	31.1	30.6	32.7	32.7
CbBl	14.0	15.9	13.7	15.9	-	15.4	14.9	14.4	14.7	14.9
StZI	49.2	50.4	48.5	50.4	-	44.5	52.6	50.5	53.3	47.3
LoLI	39.8	36.7	41.6	39.3	-	44.5	33.3	34.2	36.8	38.2
LoL/Stz(%)	81.0	72.8	85.7	78.0	-	100.0	63.3	67.9	69.0	80.8

modified region wide, fleshy, with transversely grooved ridges; without distinct median furrow (Fig. 3C). Hectocotylised arm not markedly attenuate distally.

Tentacular club similar length in males and females; ClLI males 32.8–37.6–46.6 (SD, 4.4), females 34.8–39.2–45.8 (SD, 3.9). Club crescent-shaped; sucker-bearing face convex. Club with 12–15 suckers in transverse rows, ClRC males 12–15, females 14–15; 42–60 suckers in longitudinal series, TrRC males 42–50–60 (SD, 6), females

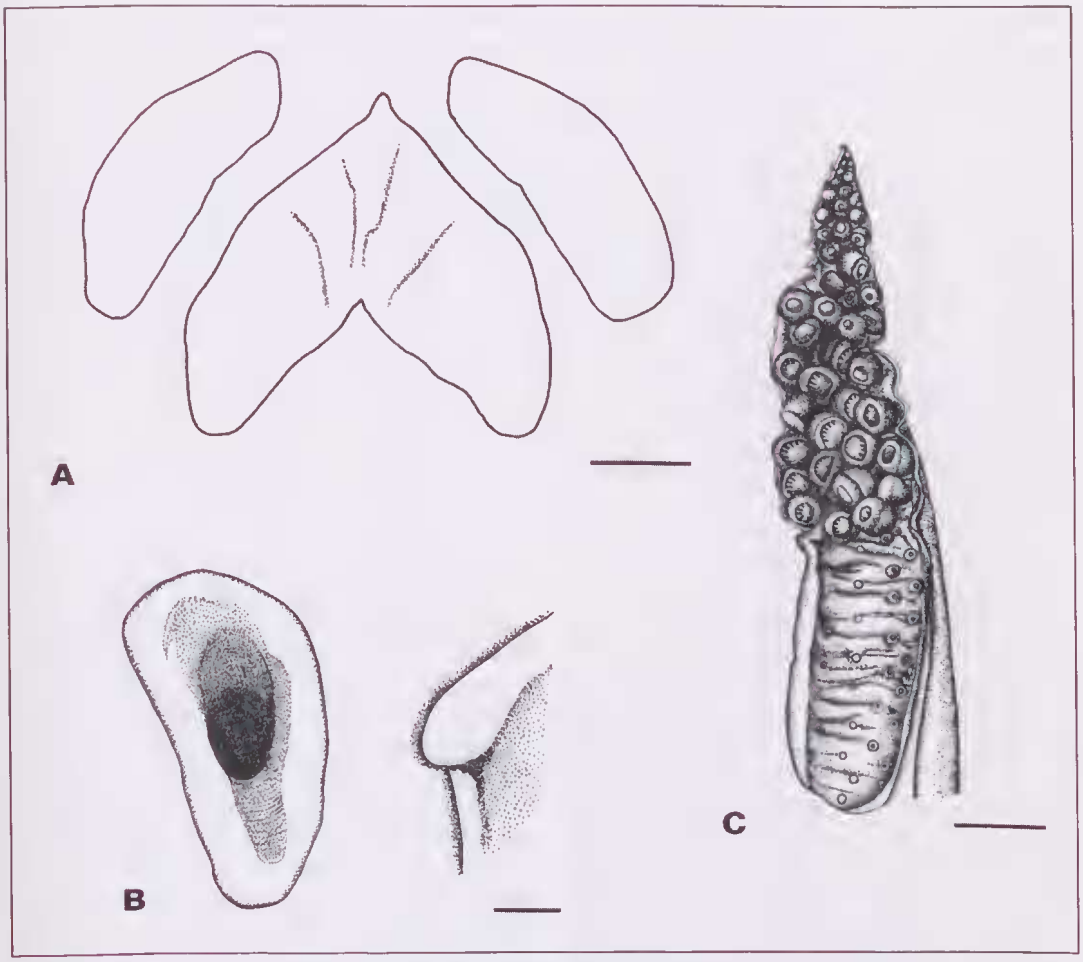

Fig. 3. *Sepiella mangkangunga* sp. nov.: **A**, funnel organ, male, NTM P11116, 37.3 mm ML, scale bar 2 mm; **B**, funnel locking cartilage (left), and mantle locking cartilage (right), female, MV F65576, 44.8 mm ML, scale bar 1 mm; **C**, hectocotylus, male, MV F65574, 52.5 mm ML. scale bar 3 mm.

48–52–54 (SD, 2). Suckers all similar size, minute (Fig. 5); ClSl males 0.55–0.61–0.69 (SD, 0.05), females 0.44–0.56–0.77 (SD, 0.13); dorsal and ventral marginal longitudinal series of suckers similar in size; ClSId males 0.43–0.51–0.61 (SD, 0.06), females 0.38–0.46–0.59 (SD, 0.07); ClSIv males 0.45–0.52–0.64 (SD, 0.06), females 0.39–0.53–0.79 (SD, 0.16). Sucker dentition: half inner ring circumference in both sexes with elongate, rectangular teeth (Fig. 4D), remaining half with blunt projections; infundibulum with approximately 7–10 hexagonal processes with elongate pegs (Fig. 4B–D); at periphery, processes smaller, flattened, without pegs (Fig. 4C, D). Swimming keel of club shorter than carpus (Fig. 5). Dorsal and ventral protective membranes not fused at base of club; joined to stalk; dorsal and ventral membranes same length, extend beyond carpus along stalk; dorsal membrane forms shallow cleft at junction with stalk.

Gills with 25–30 lamellae per demibranch; GiLC males 25–25–26 (SD, 0.5), females 25–27–30 (SD, 2). Gill length: GiLI males 25.0–33.4–41.9 (SD, 5.7), females 22.2–33.4–46.2 (SD, 7.2).

Buccal membrane without suckers. Upper beak (Fig. 6A) rostrum sharply pointed, long, curved, length greater than width, cutting edge straight; hood high above crest posteriorly; wings and hood narrow, short;

Table 4. *Sepiella mangkangunga* sp. nov.; ranges of arm length indices (ALI), arm sucker diameter indices (ASIn) and arm sucker counts (ASC) of 10 mature males and 10 mature females. min. = minimum, max. = maximum, SD = standard deviation.

	Males				Females			
	min.	mean	max.	SD	min.	mean	max.	SD
ALI1	36.5	47.4	62.7	7.7	28.6	37.9	48.8	7.3
ALI2	39.9	48.8	56.0	4.8	29.9	39.7	48.8	6.6
ALI3	46.9	55.4	65.5	6.1	33.5	41.3	50.8	6.3
ALI4	50.4	60.5	73.5	7.3	34.7	44.3	57.5	8.9
ASIn1	2.29	2.80	3.25	0.32	0.92	1.55	2.08	0.31
ASIn2	2.50	2.73	2.99	0.20	1.23	1.59	1.84	0.21
ASIn3	2.37	2.64	3.10	0.20	1.31	1.56	1.75	0.14
ASIn4	2.08	2.60	2.85	0.21	1.37	1.57	1.84	0.19
ASC1	60	70	76	5	88	98	108	5
ASC2	64	73	82	5	98	109	120	8
ASC3	82	90	98	5	104	116	130	8
ASC4	78	87	94	5	90	108	126	10

jaw angle approximately 90°; hood dark brown, fading toward lateral ventral margin, crest dark brown medially, paler brown laterally. Lower beak (Fig. 6B–C) rostral edge curved; rostrum protruding only slightly; hood low on crest; crest straight; no indentation on lateral wall edge; hood and wings width narrow; hood notch absent; wings widely spaced; crest wide; rostrum pigmented dark brown, fading on wings, crest pigmented, darkest medially. Radula homodont; rhachidian teeth with truncate bases, blunt, triangular, sides straight (Fig. 4E–F); first lateral teeth slightly longer than rhachidian teeth, broader with wide heels, assymetrical with mesocone displaced toward centre of radula (Fig. 4E–F); second laterals longer than first, curved with broad heels; marginal teeth elongate, tapering, curved (Fig. 4E). Digestive tract: (Fig. 6D) paired salivary glands approximately 1/4 length of buccal mass; paired digestive glands large, located close together, with triangular lobes posteriorly, ducts (not shown in Fig. 6) connect digestive glands near midline with caecum, ducts with branched attached pancreatic tissue; oesophagus running dorsally along median junction of digestive glands, joining sac-like stomach immediately posterior to digestive glands; caecum disc-like, grooved in blunt V-shape anteriorly, surface lining finely pleated; intestine undifferentiated; ink sac and anal flaps well developed.

Male reproductive tract: testis on left posterior side of viscero-pericardial coelom; at distal end, convoluted vas deferens opening into broad, cone-shaped mucilaginous gland, then narrower, curved, spermatophoric gland (Fig. 7A). Close to junction with lobe-shaped accessory gland and gland appendix, delicate ciliated canal joining spermatophoric gland; distal deferent canal connects appendix of accessory gland to spermatophoric sac; genital orifice opening dorsal to left gill in anterior end of mantle cavity. Spermatophores: cement body bipartite (Figs 7B, 8A–B); aboral end cylindrical, tapering toward oral end, connecting to sperm reservoir via narrow duct extending from nipple-like tip of cement body, connects to oral end by distinct fold; oral end narrower than aboral end, tapering; ejaculatory apparatus coiled, extending into oral dilation of spermatophore. Spermatophores 3.3–5.0 mm long (SD, 0.58), 0.10–0.15 mm wide (SD, 0.01); SpLI 7.6–8.3–8.7 (SD, 0.4); SpWI 0.23–0.25–0.26 (SD, 0.01).

Female reproductive tract: ovary hangs from dorsal wall of posterior viscero-pericardial coelom. Oviduct thin-walled, continuous with body cavity; distally with thickened, glandular walls (oviducal glands). Nidamental glands in mature animals occupy large portion of ventral side of mantle cavity. Accessory nidamental glands

Table 5. Morphological parameters showing sexual dimorphism in *Sepiella mangkangunga* sp. nov. Regression data relating to Figure 11 where $Y = a + bX$ where Y = dependent variable, a = intercept, b = slope, X = ML. Sig. = significant difference between the regression lines of males (M) and females (F) with respect to intercept, N = number of specimens, r^2 proportion of total variation accounted for by regression.

Y	Sex	N	r^2	a	b	Sig.
AL3	M	10	0.477	7.53	0.384	P<0.01
	F	10	0.086	10.20	0.221	
AS1	M	10	0.572	0.20	0.023	P<0.001
	F	10	0.446	-0.72	0.029	
AS2	M	10	0.792	0.04	0.026	P<0.001
	F	10	0.452	-0.27	0.021	
AS4	M	10	0.580	0.43	0.016	P<0.001
	F	10	0.630	-0.57	0.026	
CbW	M	9	0.878	2.17	0.240	P<0.001
	F	8	0.881	1.33	0.283	
StZ	M	9	0.909	-7.03	0.693	P<0.001
	F	9	0.819	-4.84	0.592	

anterior to nidamental glands (Fig. 7C). Eggs spherical, 1.6–2.8 mm diameter (SD, 0.4); EgDI 2.8–4.2–5.2 (SD, 0.8).

Subdermal cartilaginous layer between cuttlebone and skin absent. Cuttlebone length approximately equal to mantle length; outline oblong, widest medially, tapers toward either end (Fig. 9A–B); CbL males 36.0–41.1–47.7 (SD, 4.5), females 42.7–51.1–57.0 (SD, 4.8); CbWI males 29.1–30.8–33.0 (SD, 1.3), females 23.2–31.2–33.5 (SD, 3.2); strongly convex in lateral view (Fig. 9C); CbBI males 11.9–14.7–15.8 (SD, 1.1), females 13.7–14.8–15.9 (SD, 0.9). Bone bluntly rounded anteriorly and posteriorly; strongly recurved ventrally. Dorsal surface creamy white; evenly convex; texture smooth, not pustulose. Dorsal median rib present, distinct, broadening anteriorly; lateral ribs absent. Chitin surrounding entire margin of cuttlebone. Spine absent. Striated zone convex; StZI males 48.6–52.0–56.0 (SD, 3.0), females 44.5–49.6–53.3 (SD, 2.7). Last loculus convex; LoLI males 28.5–37.1–40.6 (SD, 4.1), females 33.3–38.3–44.5 (SD, 3.5); approximately 2/3 length of striated zone at midline, LoL/StZ(%) males 50.9–71.8–82.9 (SD, 11.0), females 63.3–77.6–100.0 (SD, 11.1); loculus extending posteriorly as narrow margin on each side of striated zone. Sulcus extending along striated zone only; shallow, wide; flanked by rounded ribs. Last loculus with pronounced median indentation. Anterior striae inverted U-shape, slightly wavy (Fig. 9B). Limbs of inner cone short, extend anteriorly to junction of striated zone and posterior termination of last loculus. Inner cone limbs narrow anteriorly, broaden slightly posteriorly; thickened; not raised to form ledge posteriorly (Fig. 9D). Outer cone chitinous, spatulate, expanded; narrow anteriorly, broadening posteriorly; posterio-lateral wall with pronounced indentation in males and slight indentation in females; limbs expanded, extending posteriorly beyond inner cone, recurved ventrally (Fig. 9C–D).

Papillae absent. Colour (alcohol preserved specimens): head and arms with few scattered chromatophores (Fig. 2A); dorsal mantle pale, peppered with scattered purple-black chromatophores; paired dorsal eye spots absent. Fins pale; without markings at base. Ventral pigment absent (Fig. 2B).

Distribution. Australia: Northern Territory, 12°48'S 130°21'E to 13°14'S 130°57'E (Fig. 10). Bones collected from Melville Is., Condon Bay, 11°35'S 131°10'E. Depth range 1.1–3.3 m. Habitat sand.

Remarks. The modification of the hectocotylus in *Sepiella mangkangunga* sp. nov. is clearly visible in all males examined here, including those deemed to be immature due to the absence of fully developed spermatophores in the spermatophoric sac. In addition to the secondary sexual modification of the hectocotylus described above, there are a number of statistically significant morphometric differences between the sexes (Fig. 11). Regression data relating to the features shown in this Figure are given in Table 5. With respect to mantle length, the length of the third arm and the diameters of the first, second and fourth arm suckers tend to be greater in males than females. With respect to cuttlebone length, the width of the cuttlebone is greater in females than in males and the length of the striated zone is greater in males than females (Fig. 11). *Sepiella mangkangunga* sp. nov.

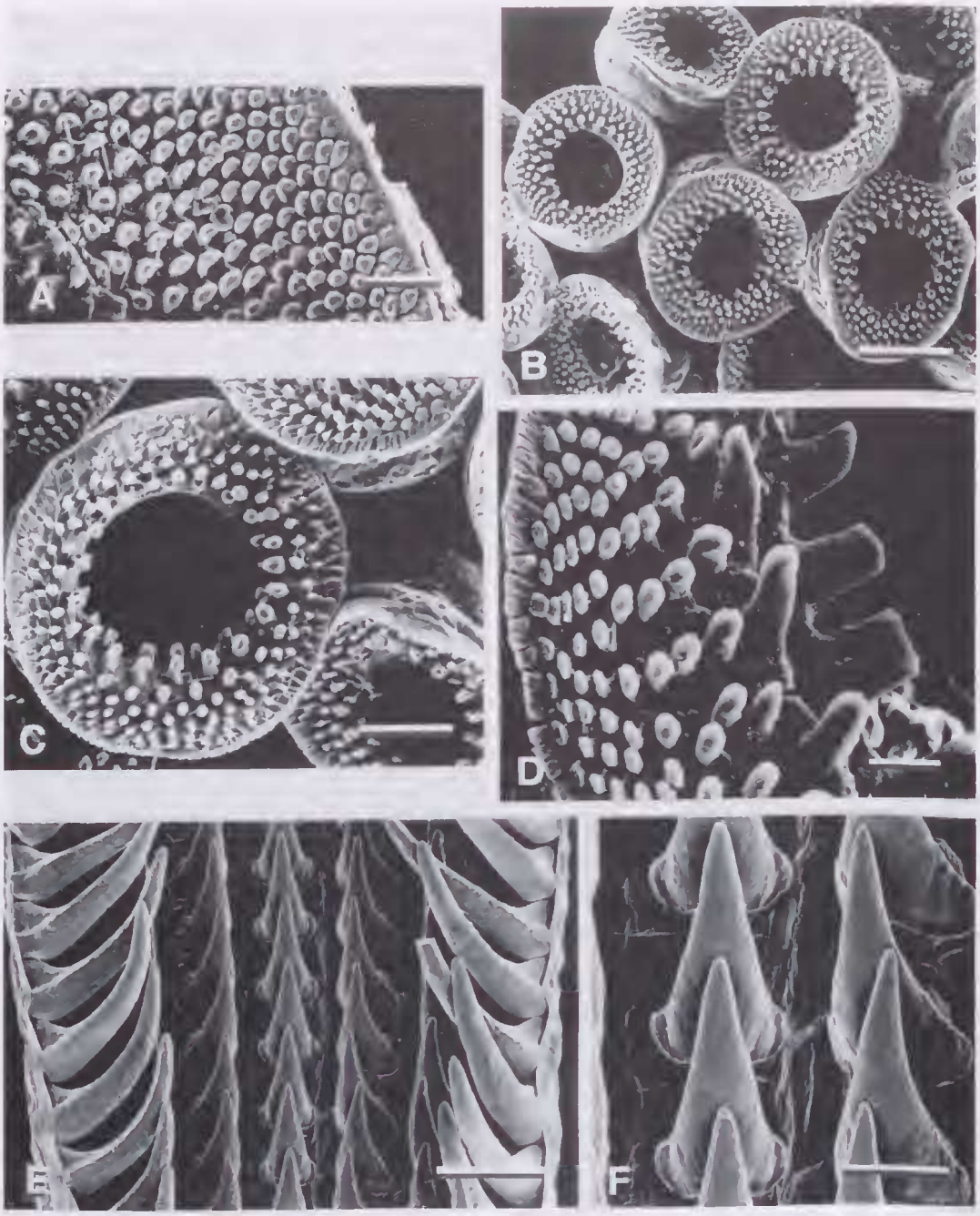

Fig. 4. *Sepiella mangkangunga* sp. nov.: **A**, sucker rim, arm 4, female, NTM P11116, 55.5 mm ML, scale bar 30 μm; **B**, club suckers, male, NTM P11116, 34.0 mm ML, scale bar 100 μm; **C**, enlargement of club sucker, same specimen, scale bar 50 μm; **D**, club sucker rim, female, NTM P11116, 55.5 mm ML, scale bar 20 μm; **E**, radula, female, NTM P11116, 57.2 mm ML, scale bar 200 μm; **F**, enlargement of rhachidian (left) and first lateral teeth (right), same specimen, scale bar 100 μm.

differs from *S. weberi* Adam in a number of characters. *Sepiella mangkangunga* sp. nov. has a greater number of club suckers in the transverse rows (CIRC 12–15) than *S. weberi* (CIRC 7–10). The club swimming keel in *S. mangkangunga* sp. nov. is shorter

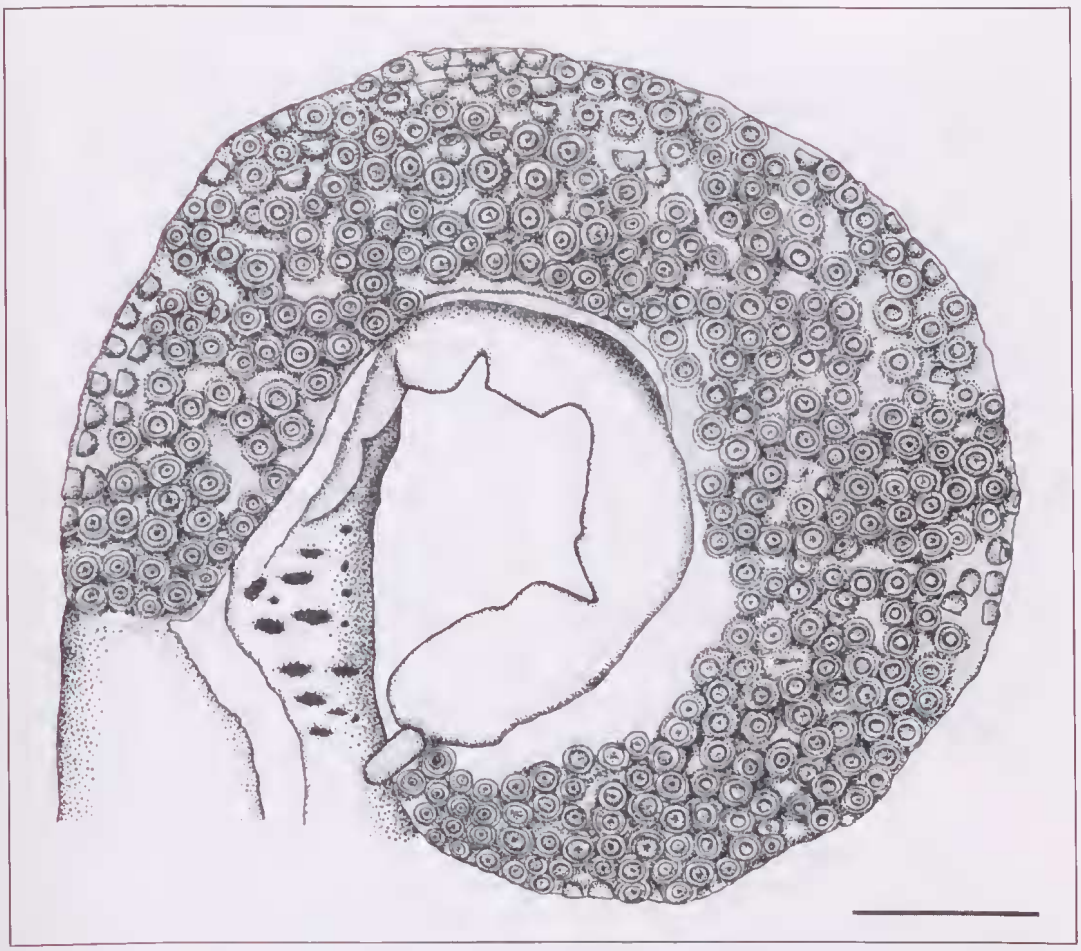

Fig. 5. *Sepiella mangkangunga* sp. nov.: tentacular club, female, NTM P11116, 54.6 mm ML, scale bar 2 mm.

than the carpus, but is the same length as the carpus in *S. weberi*. The hood notch of the lower beak is much deeper in *S. mankungunga* sp. nov. than in *S. weberi*. The cuttlebone of *S. mangkangunga* sp. nov. is broader (dorso-ventrally), and wider (perpendicular to the longitudinal axis of the cuttlebone) than the *S. weberi* cuttlebone, with a pronounced indentation in the posterio-lateral edge of the outer cone. If an indentation is present at all in the outer cone, it is not very pronounced in *S. weberi* (compare Figs 9 and 19). The depression in the last loculus is more pronounced in *S. mangkangunga* sp. nov. than in *S. weberi*. The inner cone is thicker in *S. mangkangunga* sp. nov. than in *S. weberi* (Figs 9D and 19D), though this difference may be difficult to detect in small specimens. In addition, the distinctive ovoid spots along the base of the fins in *S. weberi* are not seen in *S. mangkangunga* sp. nov. The latter species is found in shallow water (1.1–3.3 m), while *S. weberi* occurs at depths of 77–88 m in Australian waters (though it has been collected in shallower water elsewhere). Some differences between *S. mangkangunga* sp. nov. and other nominal species in the genus are summarised in Table 6. *Sepiella mangkangunga* sp. nov., with *S. japonica* Sasaki, 1929, differs from other nominal *Sepiella* in the absence of ovoid spots at the base of the fins. *Sepiella japonica* however, has white spots on the mantle and a whitish line along the fin bases (though these may be indistinct in preserved specimens), unlike *Sepiella mangkangunga* sp. nov., and a greater number of suckers in transverse rows

on the club (Table 6). *Sepiella mangkangunga* sp. nov. occurs in close geographic proximity to Melville Island, the type locality of *S. melwardi* Iredale, 1954 (Fig. 11). *Sepiella melwardi* was described from cuttlebones collected on the island, but was subsequently synonymised by Lu (1998) with *S. weberi*. Iredale (1954) noted that the cuttlebones collected on Melville Island were clearly separable into two morphological types. Iredale (1954) attributed these differences to sexual dimorphism and designated one, from a supposed female, as the name-bearing type. The second specimen (AM C133321), described by Iredale (1954) as a male *S. melwardi*, is in fact *S. mangkangunga* sp. nov.

Etymology. The specific name, *mangkangunga*, is a Murrinh-Patha Aboriginal word used for cuttlefish (Walsh 1994). Murrinh-Patha is spoken by the population of Wadeye located on the western coast of the Northern Territory. Gender feminine.

Sepiella weberi Adam, 1939
(Figs 12–19; Tables 6–8)

Sepiella weberi Adam, 1939: 98 – 101, plate IV, figs 1-2; text figs 6-8.

Sepiella melwardi Iredale, 1954: 78–79 (in part), plate V, figs 1–3.

Type material. SYNTYPES – (ZMA Moll. 3.39.001), Soemba - F (69.3 mm ML), 10°S 119°56'E, 18.3 m (10 fathoms), 19 February 1909, coll. Siboga Expedition; (ZMA Moll.2.39.002), Timor, off Kupang, M (59.7 mm ML); 8°35'S 126°00'E, surface (attracted to lamplight), 22 January 1909, coll. Siboga Expedition.

Additional material. Australia: Northern Territory – 1 cuttlebone (53.0 mm CbL), Melville Is., Condon Bay, 11°35'S 131°10'E, on beach, coll. M. Ward, (AM C133320) (holotype of *S. melwardi*); Western Australia – 6F (47.1–58.0 mm ML), 12°39'S 127°03'E – 12°39'S 127°06'E, 88 m, 25 March 1981, coll. RV *Hai-Kung*, (MV F65575); 1M (56.8 mm ML), North West Shelf, 12°40'S 12°12'E – 12°40'S 127°09'E, 88–86 m, 25 February 1981, coll. C.C. Lu on RV *Hai Kung*, (MV F65571); 1M (44.5 mm ML), (MV F65579); 7F (47.0–57.8 mm ML), (MV 71713); 1F (52.0 mm ML) 19°35'S 117°12'E – 19°35'S 117°14'E, 79–77 m, 10 March 1981, coll. M.F. Gomon on RV *Hai-Kung*, (MV F65577).

Diagnosis. Club with 7–10 suckers in transverse rows; swimming keel, and club protective membranes terminate at level of carpus. Dorsal mantle with five to six ovoid spots at base of each fin in both sexes. Cuttlebone not strongly convex in lateral view; posterio-lateral margin of outer cone without pronounced indentation.

Description. Counts and indices for individual specimens are given in Table 7; ranges for arm length indices, arm sucker diameter indices and arm sucker counts are shown in Table 8.

Small to moderate sized species; ML males 44.5–50.7–56.8 **59.7** (SD, 8.7), females 48.0–52.2–58.0 **69.3** (SD, 3.5). Mantle oblong; MWI males 52.8–54.5–56.2 (SD, 2.4), females 45.0–51.5–55.2 (SD, 4.1); dorsal anterior margin triangular, obtuse; extending anteriorly to level of middle of eyes (Fig. 12A); AMHI males 11.5–11.9–12.3 (SD, 0.6), females 8.7–10.6–12.9 (SD, 1.7). Ventral mantle margin emarginate, without distinct lateral angle (Fig. 12B); VMLI males 82.5–84.0–85.6 (SD, 2.2), females 80.2–84.0–85.8 (SD, 2.2). Fins widest in posterior third; FWI males 10.3–11.4–12.5 (SD, 1.5), females 10.0–12.6–15.8 (SD, 2.2); anterior origin posterior to mantle margin; FIIa males 11.4–12.5–13.5 (SD, 1.4), females 9.8–12.9–16.9 (SD, 2.8); ending in lobes which lie very close together; narrow gap between fins; FIIp males 4.5, females 2.0–3.8–4.6 (SD, 1.0). Funnel long, broad-based; extends to anterior rim of eye; FuLI males 27.0–28.4–29.9 (SD, 2.1), females 29.5–31.2–32.3 (SD, 1.0). Funnel free portion approximately one-third funnel length; FFuI males 11.2–12.7–14.1 (SD, 2.0), females 11.8–14.4–18.5 (SD, 2.7). Funnel organ dorsal elements inverted V-

Table 6. Distinguishing features of nominal *Sepiella* species. For non-Australian material, information was obtained from: Adam (1939), Adam and Rees (1966), Khromov *et al.* (1998), Nesis (1987), Okutani (1995) and Roeleveld (1972). 'Broad' refers to the dorso-ventral breadth of the cuttlebone. For abbreviations, see Table 1. Only those characters for which information was available for most species are included. * – species of uncertain status, M – males, F – females, m – metres. † – minimum depth not known.

Species	Patches at base of fins	ClRC	CbW/CbL	Broad cuttlebone	Maximum size (mm ML)	Depth range	Type locality	Distribution
S. cyanea Robson, 1924	+	10-14	29-33%M 30-36%F	+	80	? – 75m †	South Africa 29°17'S 31°33'E	South Africa – Port Elizabeth to 26°N of Mozambique and Madagascar
S. inermis Orbigny, 1848	+	12-24 13-20	33-43%	+	125	? – 40m †	Indian Ocean	Persian Gulf – southern part of Red Sea to mouth of Zambezi River, east to eastern Indonesia, Gulf of Tonkin
S. japonica Sasaki, 1929	-	16-32 >20 (usually)	30-35%	+	200	? – 50m †	Japan	Japan (central Honshu) to China (Canton), Philippines
S. mangkangunga sp. nov	-	12-15M 14-15F	27-31%M 23-33%F	+	58M 58F	1.1 – 3.3m	Australia	Northern Australia, 12°48`S 131°21'E – 13°14'S 130°57'E
S. ocellata Pfeffer, 1884*	+	8-10	20-25%	+	50	?	Java	Known only from type
S. ornata (Rang, 1837)	+	10-14	24-27%M 27-30%F	+	100	? – 150m † usually > 50m	Gulf of Guinea	West Africa – Cape Blanco to Cape Frio
S. weberi Adam, 1939	+	8M 7-10F	21-31%M 30-33%F	-	60M 69F	surface – 88m	Timor & Soemba	Indonesia – northern Australia, 8°35'S 126°00'E -19°35'S 117°14'E

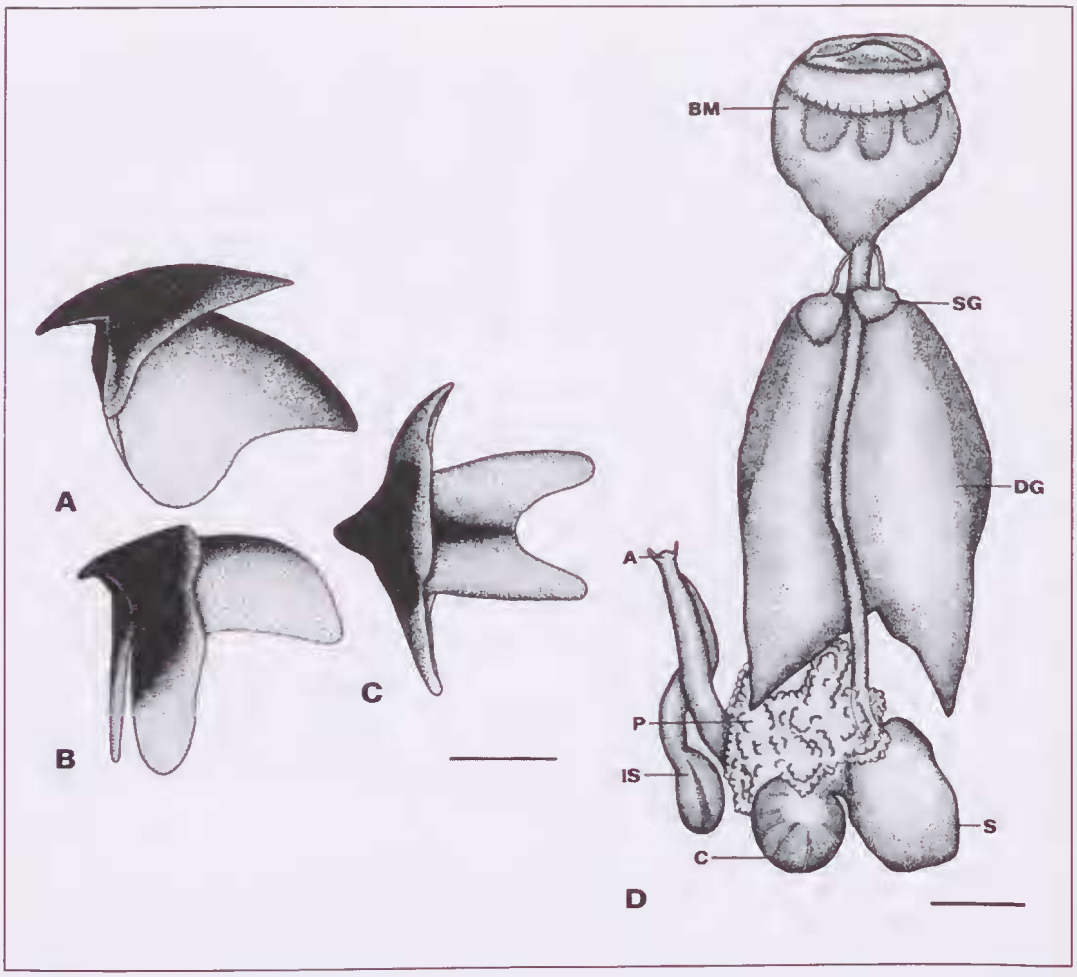

Fig. 6. *Sepiella mangkangunga* sp. nov.; **A**, upper beak, lateral view; **B**, lower beak, lateral view; **C**, lower beak, ventral view (A–C, female paratype, MV F80992, 54.7 mm ML, scale bar 2 mm); **D**, digestive tract, dorsal view, male, MV F65573, 37.7 mm ML, scale bar 3 mm (A – anus; BM – buccal mass; C – caecum; DG – digestive gland; IS – ink sac; P – pancreas; S – stomach; SG – salivary gland).

shape with low medial swelling and small papilla in front; ventral elements oval with acute anterior tip (Fig. 13A). Mantle-locking cartilage curved, with triangular tubercle; funnel-locking cartilage with depression corresponding to tubercle (Fig. 13B). Head short; HLI males 29.4–30.1–30.8 (SD, 1.0), females 27.1–29.6–31.6 (SD, 1.5); slender, narrower than mantle; HWI males 40.0–40.2–40.4 (SD, 0.3), females 32.5–36.9–41.0 (SD, 3.5). Eyes moderate size; EDI males 11.8–12.1–12.4 (SD, 0.4), females 12.6–13.4–14.6 (SD, 0.7); ventral eyelids present.

Male and female arms subequal in length (Table 8). Arm length index of longest arms in males (ALI4) 65.1–65.2–65.2 (SD, <0.01), females (ALI4) 37.9–42.8–46.9 (SD, 3.7). Protective membranes in both sexes wide, well developed; normal, not thickened. Distal arm tips in both sexes not markedly attenuate. Arm suckers tetraserial in both sexes. Two median series of suckers larger than dorsal and ventral marginal series in males; larger than female arm suckers (Table 8). Chitinous rims of arm suckers with marked sexual dimorphism. In males, distal margin of inner ring with 12–14 elongate,

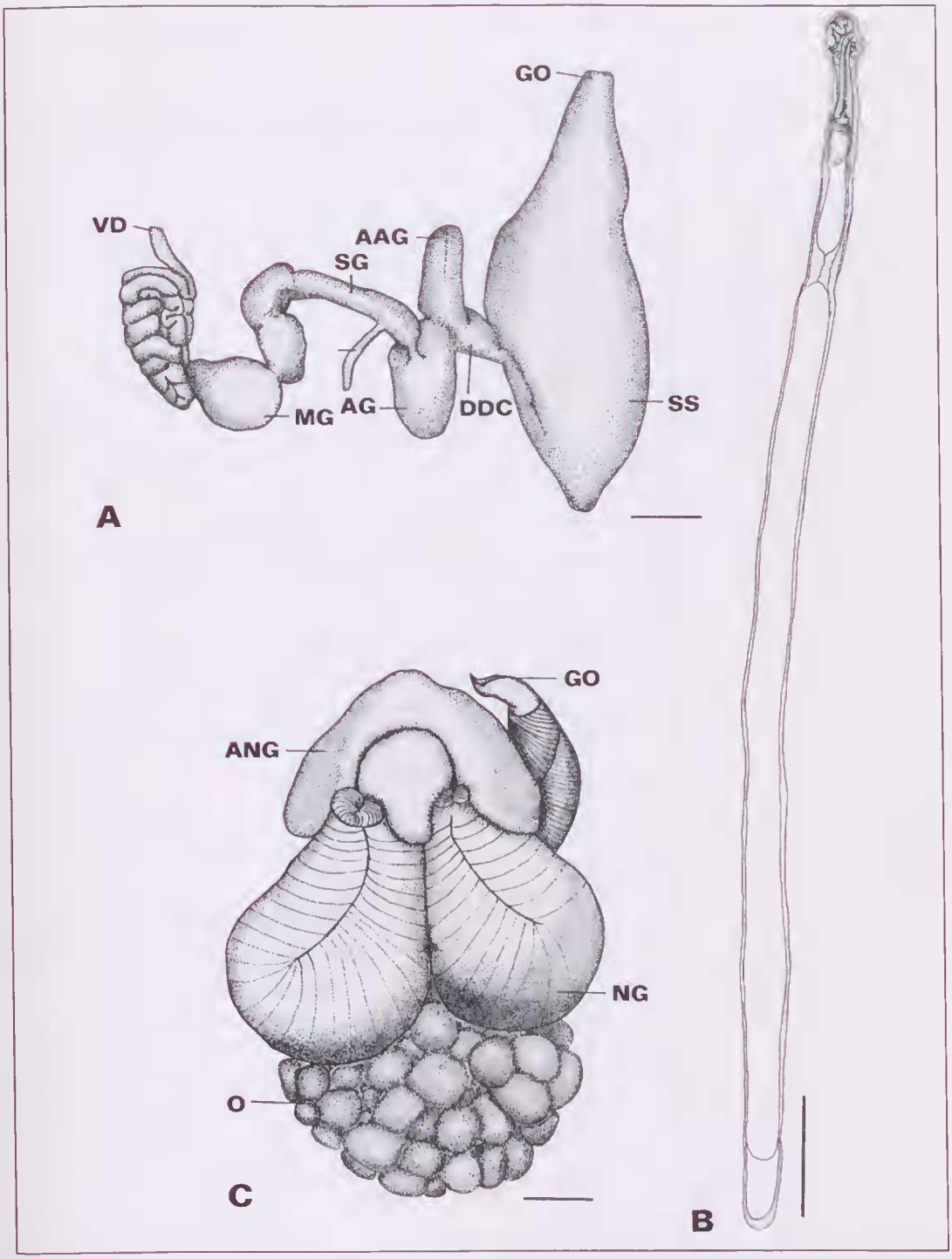

Fig. 7. *Sepiella mangkangunga* sp. nov.: **A**, male genital duct (testis not shown), paratype, MV F80992, 45.8 mm ML, scale bar 2 mm (AAG – appendix of accessory gland; AG – accessory gland; CC – ciliated canal; DDC – distal deferent canal; GO – genital orifice; MG – mucilaginous gland; SG – spermatophoric gland; SS – spermatophoric sac; VD – vas deferens); **B**, spermatophore, male, NTM P11116, 57.2 mm ML, scale bar 0.5 mm; **C**, female genital duct NTM P11116, 54.6 mm ML, scale bar 2 mm (ANG – accessory nidamental gland; GO – genital opening; NG – nidamental gland; O – ovary).

Table 7. Measurements (mm), counts and indices of 3 mature male and 7 mature female *Sepiella weberi* Adam. M – male, F – female.

Museum Reg. No.	NMV F65579 M	NMV F65571 M	ZMA Moll.2.39.002 M	NMV F71713 F	NMV F71713 F	NMV F65575 F	NMV F71713 F	NMV F71713 F	NMV F65575 F	ZMA Moll.3.39.001 F
ML	44.5	56.8	59.7	48.0	50.6	50.8	51.5	54.2	58.0	69.3
AMHl	11.5	12.3	10.0	10.2	8.9	8.7	12.0	12.9	10.9	10.4
VMLl	82.5	85.6	85.6	85.6	85.0	84.8	82.5	85.8	80.2	86.0
MWI	56.2	52.8	45.2	55.2	50.4	53.7	53.4	-	45.0	39.4
FWI	10.3	12.5	14.4	12.7	15.8	-	11.3	10.0	13.3	15.3
AFII	13.5	11.4	10.0	16.9	10.9	9.8	15.5	12.9	11.2	8.4
PFII	4.5	-	3.3	4.2	2.0	4.1	3.9	4.6	-	2.3
FuLI	27.0	29.9	26.0	32.3	30.6	31.5	31.1	29.7	31.9	20.9
FFuI	11.2	14.1	18.4	15.6	15.8	11.8	12.6	18.5	12.1	14.7
HLI	30.8	29.4	28.5	29.2	31.6	29.9	29.3	30.4	27.1	20.0
HWI	40.4	40.0	40.4	41.0	34.6	40.9	35.9	32.5	36.2	38.8
EDI	12.4	11.8	11.8	13.5	14.6	12.8	12.6	13.3	13.4	12.3
AL1I	40.4	38.7	33.5	35.4	33.6	40.4	38.8	35.1	29.3	34.6
AL2I	48.3	44.0	39.4	41.7	33.6	37.4	35.9	34.1	31.0	36.8
AL3I	53.9	54.6	44.4	43.8	37.5	35.4	40.8	36.9	34.5	36.1
AL4rI	65.2	65.1	54.4	46.9	39.5	41.3	46.6	44.3	37.9	38.2
AL41I	-	54.6	48.6	-	-	-	-	-	-	-
AS1In	1.84	1.85	1.59	1.56	1.28	1.48	1.46	1.42	1.47	1.44
AS2In	1.69	1.62	1.59	1.56	1.13	1.57	1.46	1.38	1.38	1.40
AS3In	2.13	1.85	1.54	1.77	1.38	1.48	1.46	1.42	1.21	1.10
AS4rIn	1.84	1.76	1.88	1.40	1.23	1.57	1.46	1.38	1.41	1.15
ASC1	71	84	-	98	72	104	98	110	94	-
ASC2	60	80	-	100	80	112	88	116	94	-
ASC3	94	102	78	100	92	114	106	118	112	-
ASC4	89	100	80	100	98	102	106	121	100	-
AS41In	2.36	1.76	1.76	-	-	-	-	-	-	-
AS41mIn	0.67	0.56	0.50	-	-	-	-	-	-	-
C1L	24.7	25.5	-	28.1	19.8	29.5	27.2	26.8	24.1	-
C1RC	8	8	-	8	9	7	8	8	8	10
TrRC	46	38	-	42	38	41	46	44	38	42
C1SI	0.56	0.44	-	0.56	0.40	0.49	0.49	0.46	0.55	0.43
C1SdI	0.49	0.35	-	0.52	0.30	0.53	0.39	0.41	0.43	0.36
C1SvI	0.45	0.35	-	0.56	0.40	0.49	0.43	0.46	0.52	0.36
GiLC	-	27	28	27	28	27	27	-	-	29
GiLI	40.9	35.9	36.2	36.3	33.6	29.7	35.9	-	34.8	30.3
SpLI	10.1	7.9	10.0	-	-	-	-	-	-	-
SpWI	0.27	0.21	0.16	-	-	-	-	-	-	-
EgLI	-	-	-	4.2	4.5	5.5	4.8	4.6	4.8	-
CbL	43.9	56.9	56.1	50.0	51.0	51.1	52.0	55.8	55.0	-
CbWI	30.8	21.4	31.4	30.6	31.6	31.9	32.7	30.5	32.7	-
CbBI	11.4	9.7	-	11.4	11.4	12.5	11.1	10.7	11.1	-
StZI	45.6	61.5	50.3	45.0	60.8	60.7	50.0	48.4	61.8	-
LoLI	41.0	32.5	40.8	45.0	31.4	33.3	38.5	34.1	30.9	-
LoL/Stz (%)	90.0	52.9	81.2	100.0	51.6	54.8	76.9	70.4	50.0	-

pointed tooth-like processes (Fig. 12C, D), proximal margin smooth (Fig. 12C); in females, distal half of inner ring with two to three rows tooth-like structures (Fig. 14A, C), proximal margin of inner ring with blunt projections (Fig. 14B); infundibulum in both sexes with 11–15 rows of hexagonal processes, with pegs on innermost rows, outer processes without pegs (Figs 12C, 14A–B). In males, infundibular processes on inner margin of toothed side of ring narrow, elongate (Fig. 12D). Sucker counts range from 60–121; females with higher average counts than males (Table 8).

Hectocotylus present in males, left ventral arm modified; sucker size reduced proximally (Fig. 13C), 11–12 rows of reduced suckers; suckers in two dorsal series smaller than remaining suckers; two dorsal series widely spaced, suckers markedly reduced; two ventral series close together, suckers alternate; maximum and minimum sucker diameters: ASInl4 1.76–2.06–2.36 (SD, 0.42), ASInl4m 0.12–0.14–0.16 (SD, <0.01). Oral surface of modified region wide, fleshy, with transversely grooved ridges; without distinct median furrow. Hectocotylised arm not markedly attenuate distally.

Tentacular club similar length in males and females; ClLl males 24.7–25.1–25.5 (SD, 0.6), females 19.8–25.9–29.5 (SD, 3.5). Club crescent-shaped; sucker-bearing face convex. Club with 7–10 suckers in transverse rows, ClRC males 8, females 7–10; 38–46 suckers in longitudinal series, TrRC males 38–42–46 (SD, 6), females 38–41–46 (SD, 3). Suckers all similar size, small (Fig. 15); ClSl males 0.44–0.50–0.56 (SD, 0.09), females 0.40–0.49–0.56 (SD, 0.06); dorsal and ventral marginal longitudinal series of suckers similar in size; ClSld males 0.35–0.42–0.49 (SD, 0.10), females 0.30–0.43–0.53 (SD, 0.09); ClSlv males 0.35–0.40–0.45 (SD, 0.07), females 0.40–0.48–0.56 (SD, 0.06). Sucker dentition: half inner ring circumference in both sexes with elongate, rectangular processes (Fig. 14D), remaining half with blunt projections; infundibulum with approximately 7–10 hexagonal processes with elongate pegs; at periphery, processes smaller, flattened, without pegs. Swimming keel of club length equal to length of carpus (Fig. 15). Dorsal and ventral protective membranes not fused at base of club (Fig. 15); joined to stalk; dorsal and ventral membranes same length, terminating at posterior end of carpus; dorsal membrane forms shallow cleft at junction with stalk.

Gills with 27–28 lamellae per demibranch; GiLC males 27, females 27–27–28 (SD, 0.5). Gill length: GiLl males 35.9–38.4–40.9 (SD, 3.5), females

Table 8. *Sepiella weberi* Adam; ranges of arm length indices (ALI), arm sucker diameter indices (ASIn) and arm sucker counts (ASC) of 10 mature males and 10 mature females. min. = minimum, max. = maximum, SD = standard deviation.

	Males				Females			
	min.	**mean**	**max.**	**SD**	**min.**	**mean**	**max.**	**SD**
ALI1	38.7	39.6	40.4	1.2	29.3	35.4	40.4	3.9
ALI2	44.0	46.2	48.3	3.0	31.0	35.6	41.7	3.7
ALI3	53.9	54.3	54.6	0.5	34.5	38.1	43.8	3.5
ALI4	65.1	65.2	65.2	0.01	37.9	42.8	46.9	3.7
ASIn1	1.84	1.85	1.85	<0.01	1.28	1.44	1.56	0.09
ASIn2	1.62	1.65	1.69	0.05	1.13	1.41	1.57	0.16
ASIn3	1.85	1.99	2.13	0.20	1.21	1.45	1.77	0.18
ASIn4	1.76	1.80	1.84	0.06	1.23	1.41	1.57	0.11
ASC1	71	77	84	9	72	96	110	13
ASC2	60	70	80	14	80	98	116	14
ASC3	94	98	102	6	92	107	118	10
ASC4	89	94	100	8	98	104	121	8

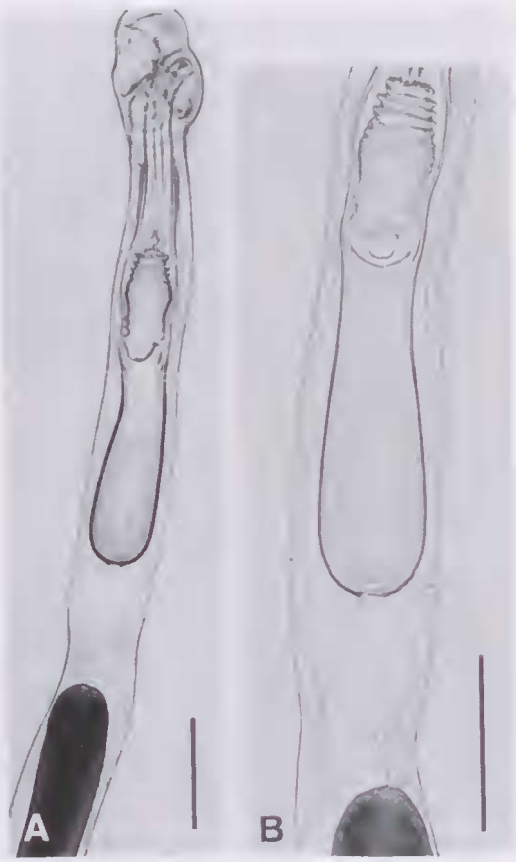

Fig. 8. *Sepiella mangkangunga* sp. nov.: **A**, spermatophore, oral end, male, NTM P16082, 57.2 mm ML, scale bar 0.3 mm; **B**, enlargement of ejaculatory apparatus, same specimen, scale bar 0.2 mm.

29.7–34.1–36.3 (SD, 2.6).

Buccal membrane without suckers. Upper beak (Fig. 16A) rostrum sharply pointed, long, curved, length greater than width, cutting edge straight; hood high above crest posteriorly; wings and hood narrow, short; jaw angle approximately 90°, slightly acute; hood dark brown, fading toward lateral ventral margin, crest dark brown medially, paler, brown laterally. Lower beak (Fig. 16B, C) rostral edge curved; rostrum protruding only slightly; hood low on crest; crest straight; no indentation on lateral wall edge; hood and wings width narrow; hood notch broad; wings widely spread; crest wide; rostrum pigmented dark brown, fading on wings, crest pigmented, darkest medially. Radula homodont; rhachidian teeth with truncate bases; blunt, triangular, sides straight (Fig. 14E–F); first lateral teeth slightly longer than rhachidian teeth, with wide heels, assymetrical with mesocone displaced toward centre of radula (Fig. 14E–F); second laterals longer than first, curved with broad heels; marginal teeth elongate, tapering, curved (Fig. 14E). Digestive tract: paired salivary glands approximately 1/4 length of buccal mass; paired digestive glands large, located close together, with sub-triangular lobes posteriorly (Fig. 16D), ducts (not shown in Fig. 16) connecting digestive glands near midline with caecum, ducts with branched attached pancreatic tissue; oesophagus running dorsally along median junction of digestive glands, joining sac-like stomach immediately posterior to digestive glands; caecum disc-like, grooved in blunt V-shape anteriorly, surface lining finely pleated; intestine undifferentiated; ink sac and anal flaps well developed.

Male reproductive tract: testis on left posterior side of viscero-pericardial coelom; at distal end, convoluted vas deferens (Fig. 17A) opening into broad, cone-shaped mucilaginous gland, then narrower, curved, spermatophoric gland. Close to junction with lobe-shaped accessory gland and gland appendix, delicate ciliated canal joining spermatophoric gland; distal deferent canal connects appendix of accessory gland to spermatophoric sac; genital orifice opening dorsal to left gill in anterior end of mantle cavity. Spermatophores: (Figs 17B, 18A, B) cement body bipartite; aboral end cylindrical, tapering toward oral end, connecting to sperm reservoir via narrow duct extending from nipple-like tip of cement body, connecting to oral end by a distinct fold; oral end narrower than aboral end, tapering; ejaculatory apparatus coiled, extending into oral dilation of spermatophore. Spermatophores 4.5–6.0 mm long (SD, 0.7), 0.10–0.12 mm wide (SD, 0.01); SpLI 7.9–9.3–10.1 (SD, 1.2); SpWI 0.16–0.21–0.27 (SD, 0.05).

Female reproductive tract: ovary hanging from dorsal wall of posterior viscero-pericardial coelom. Oviduct thin-walled, continuous with body cavity; distally with thickened, glandular walls (oviducal glands). Nidamental glands in mature animals

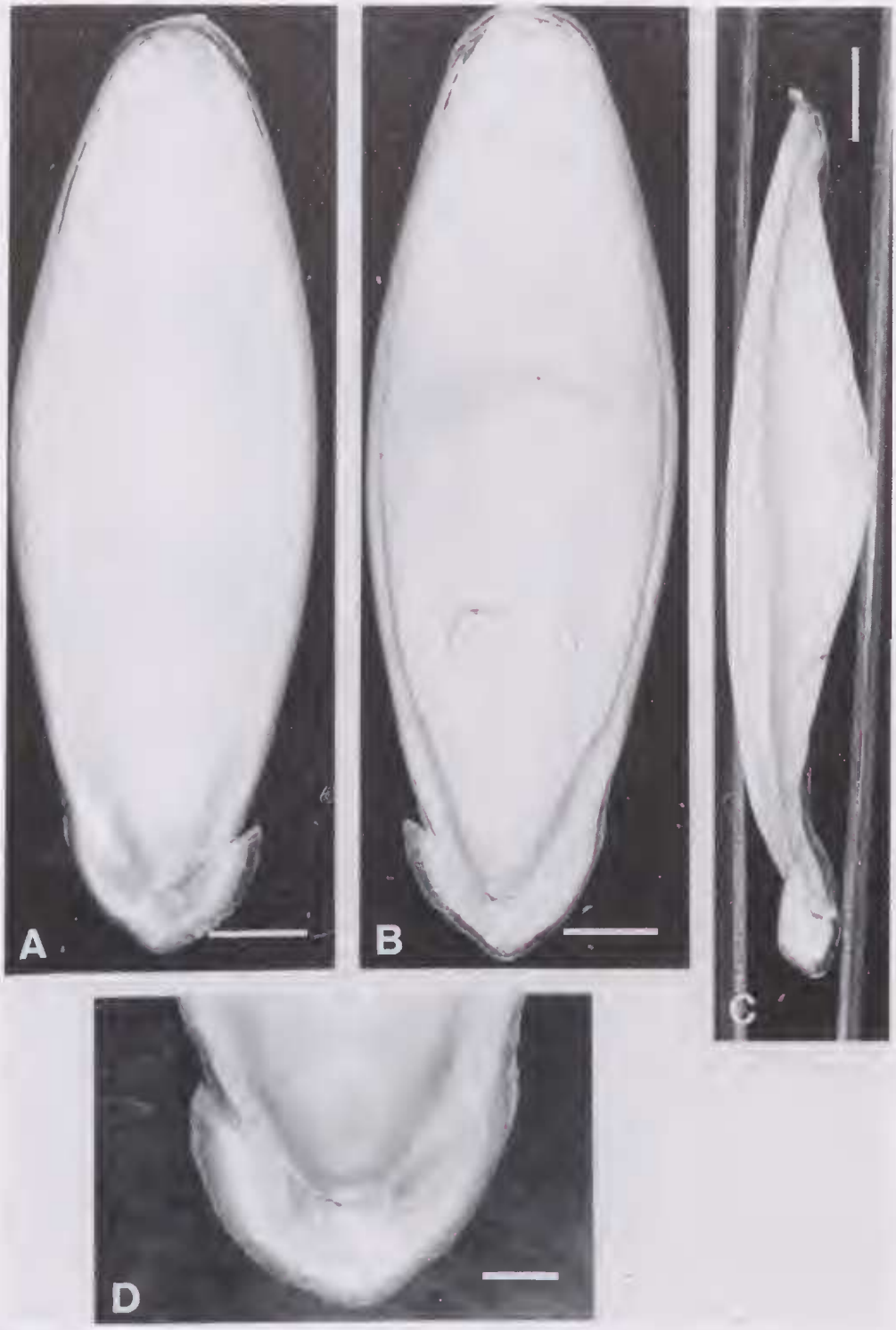

Fig. 9. *Sepiella mangkangunga* sp. nov.: **A**, cuttlebone, dorsal view, female paratype, NTM P16082, 52.2 mm ML, scale bar 5 mm; **B**, cuttlebone, ventral view, same specimen; **C**, cuttlebone, lateral view same specimen, scale bar 5 mm; **D**, posterior end of cuttlebone, ventral view, same specimen, scale bar 2 mm (n.b. bone damaged on right side with evidence of repair).

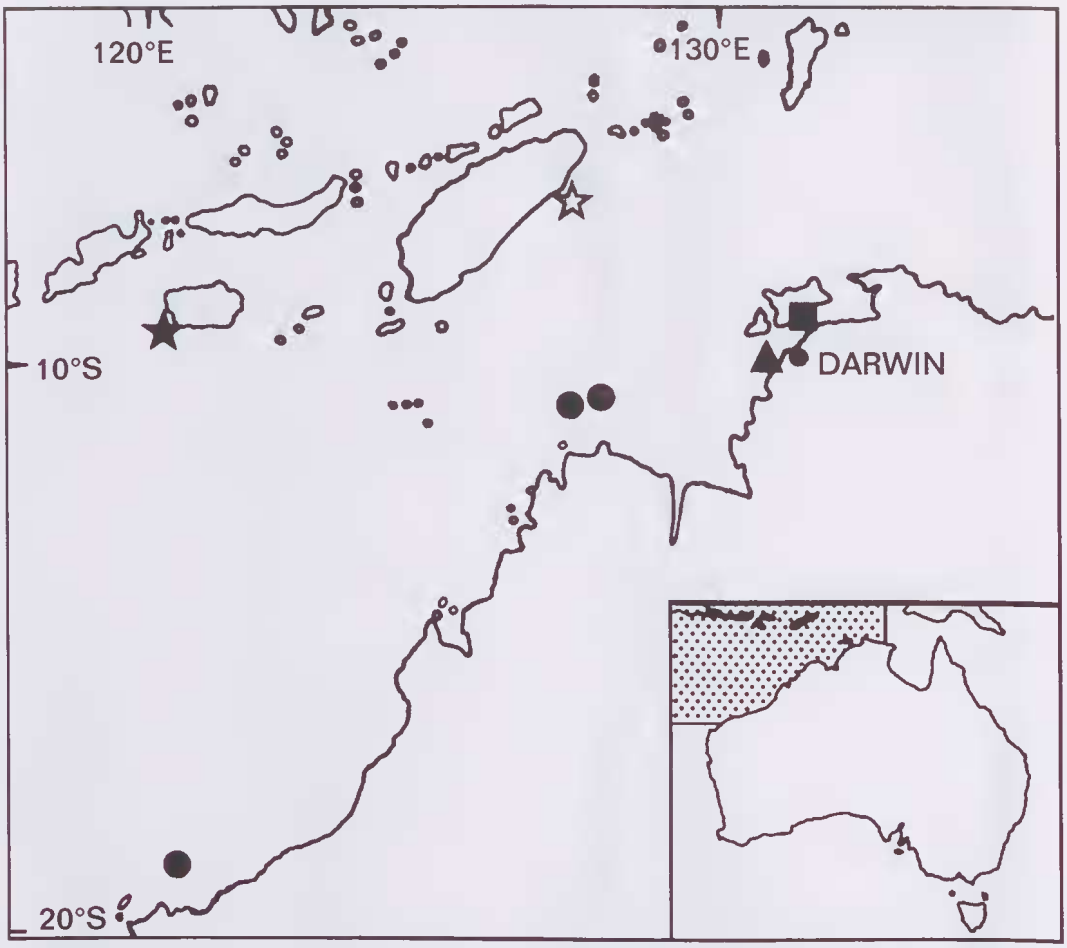

Fig. 10. Distributions of *Sepiella mangkangunga* sp. nov. (triangle), and *Sepiella weberi* Adam, 1939 (solid dots). The open star indicates the collection locality of the male, and the closed star the collection site for the female *Sepiella weberi* syntype. The solid square indicates the type locality of *Sepiella melwardi*.

occupying large portion of ventral side of mantle cavity. Accessory nidamental glands anterior to nidamental glands (Fig. 17C). Eggs spherical, 2.0–2.8 mm diameter (SD, 0.3); EgDI 4.2–4.7–5.5 (SD, 0.2).

Subdermal cartilaginous layer between cuttlebone and skin absent. Cuttlebone length approximately equal to mantle length; outline oblong (Fig. 19A, B); CbL males 43.9–50.4–56.9 (SD, 9.2), females 50.0–52.5–55.8 (SD, 2.4); CbWI males 21.4–26.1–30.8 (SD, 6.6), females 30.5–31.7–32.7 (SD, 1.0); not strongly convex in lateral view (Fig. 19C); CbBI males 9.7–10.3–11.0 (SD, 0.6), females 10.7–11.4–12.5 (SD, 0.6). Bone acuminate, acute anteriorly; bluntly rounded posteriorly; strongly recurved ventrally. Dorsal surface creamy white; convex medially, flat laterally; texture smooth, not pustulose. Dorsal median rib present, indistinct, broadening anteriorly; lateral ribs absent. Chitin surrounding entire margin of cuttlebone. Spine absent. Striated zone convex; StZI males 45.6–53.5–61.5 (SD, 11.3), females 45.0–54.4–61.8 (SD, 7.5). Last loculus convex (Fig. 19C); LoLI males 32.5–36.8–41.0 (SD, 6.0), females 30.9–35.5–45.0 (SD, 5.4); approximately 2/3 length of striated zone at midline,

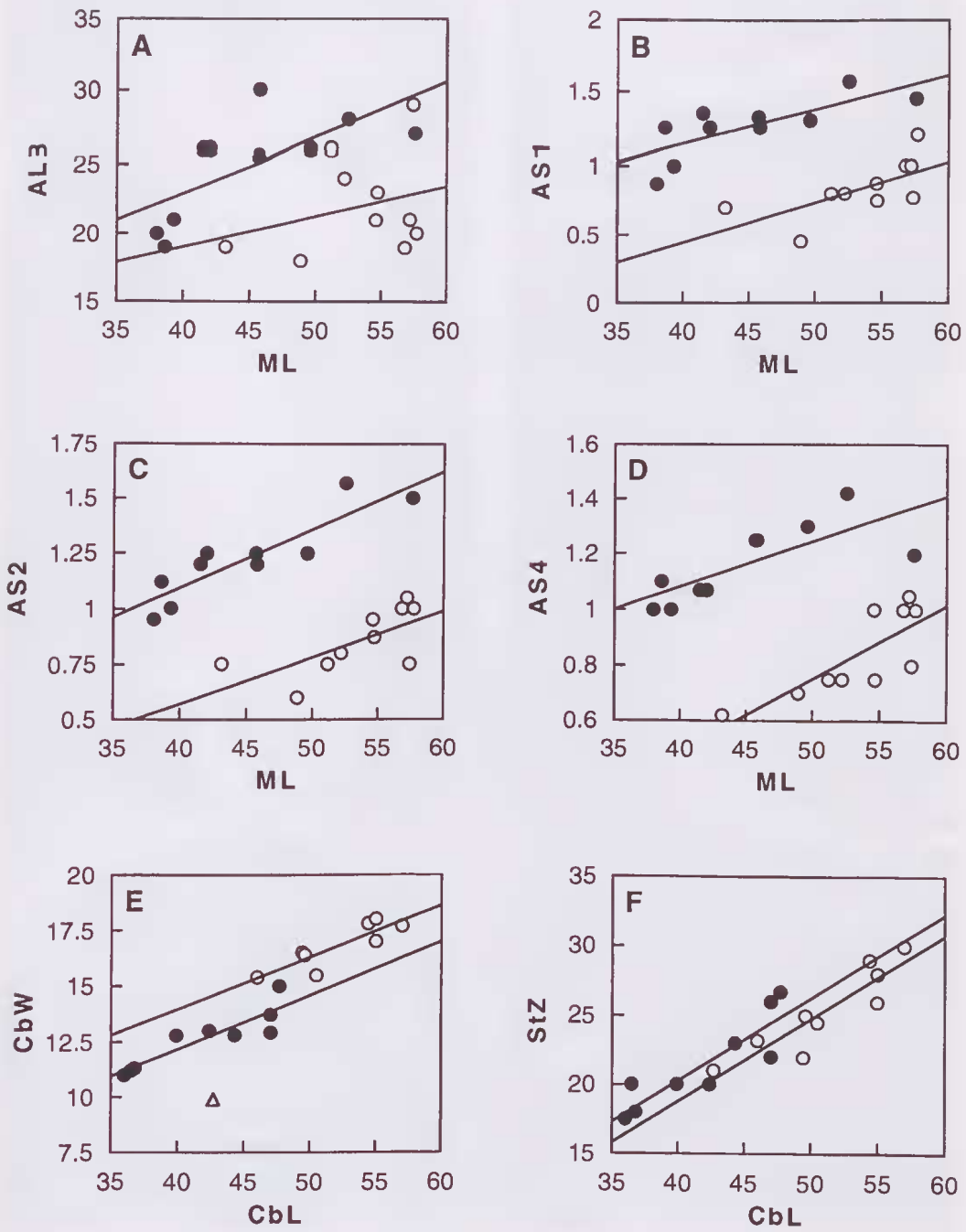

Fig. 11. Sexual dimorphism in *Sepiella mangkangunga* sp. nov. **A**, AL3 vs ML; **B**, AS1 vs ML; **C**, AS2 vs ML; **D**, AS4 vs ML; **E**, CbW vs ML; **F**, StZ vs ML. For regression formulae and comparison of lines refer to Table 5. Solid circles = males, open circles = females, open triangle (E) female – outlying value not included in the regression equation. For abbreviations see Table 1.

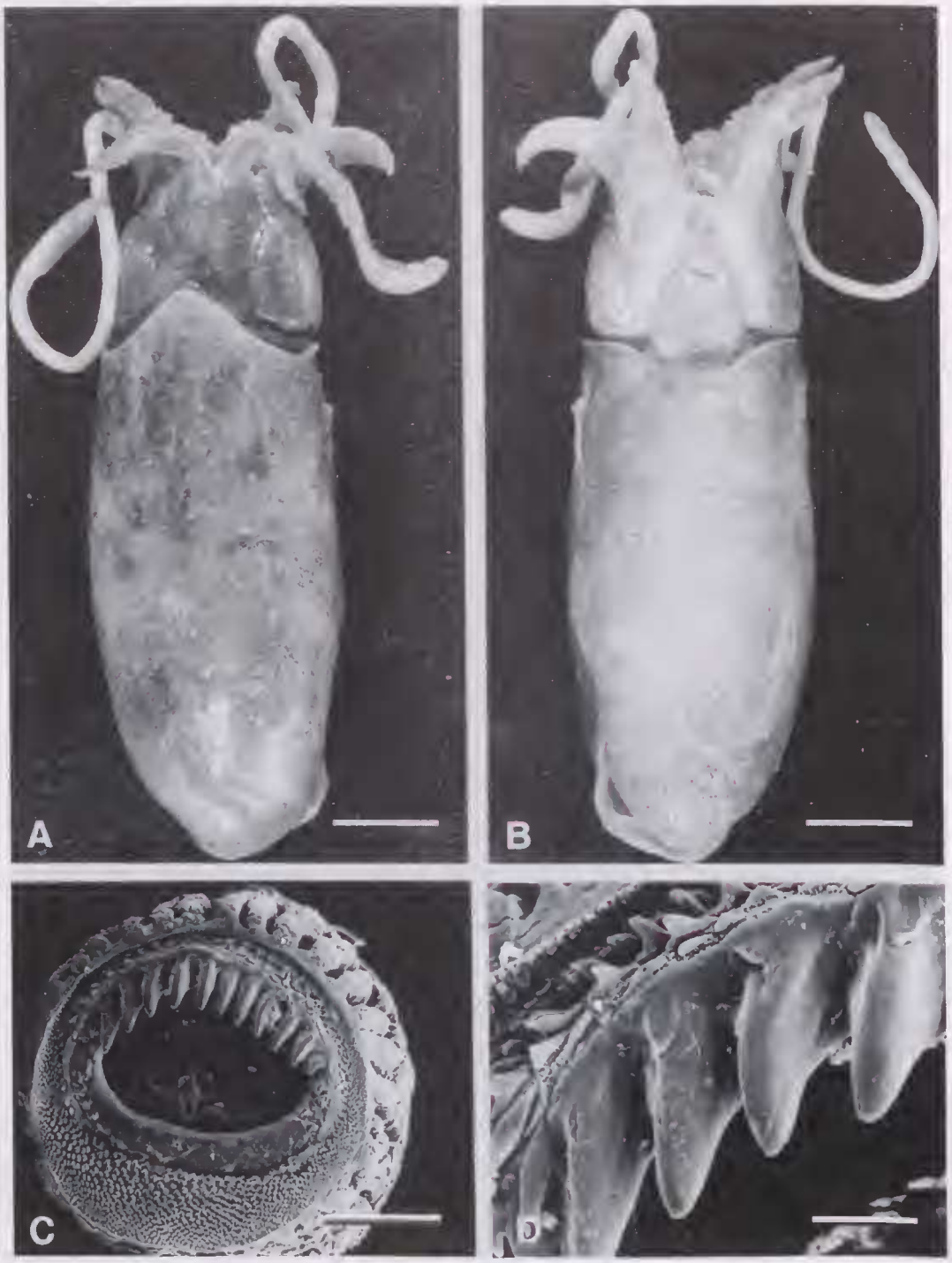

Fig. 12. *Sepiella weberi*: **A**, dorsal view, female, MV F65575, 54.3 mm ML, scale bar 10 mm; **B**, ventral view same specimen; **C**, arm 2 sucker, male, MV F65571, 56.8 mm ML, scale bar 200 μm; **D**, enlargement of sucker rim, same specimen, scale bar 40 μm.

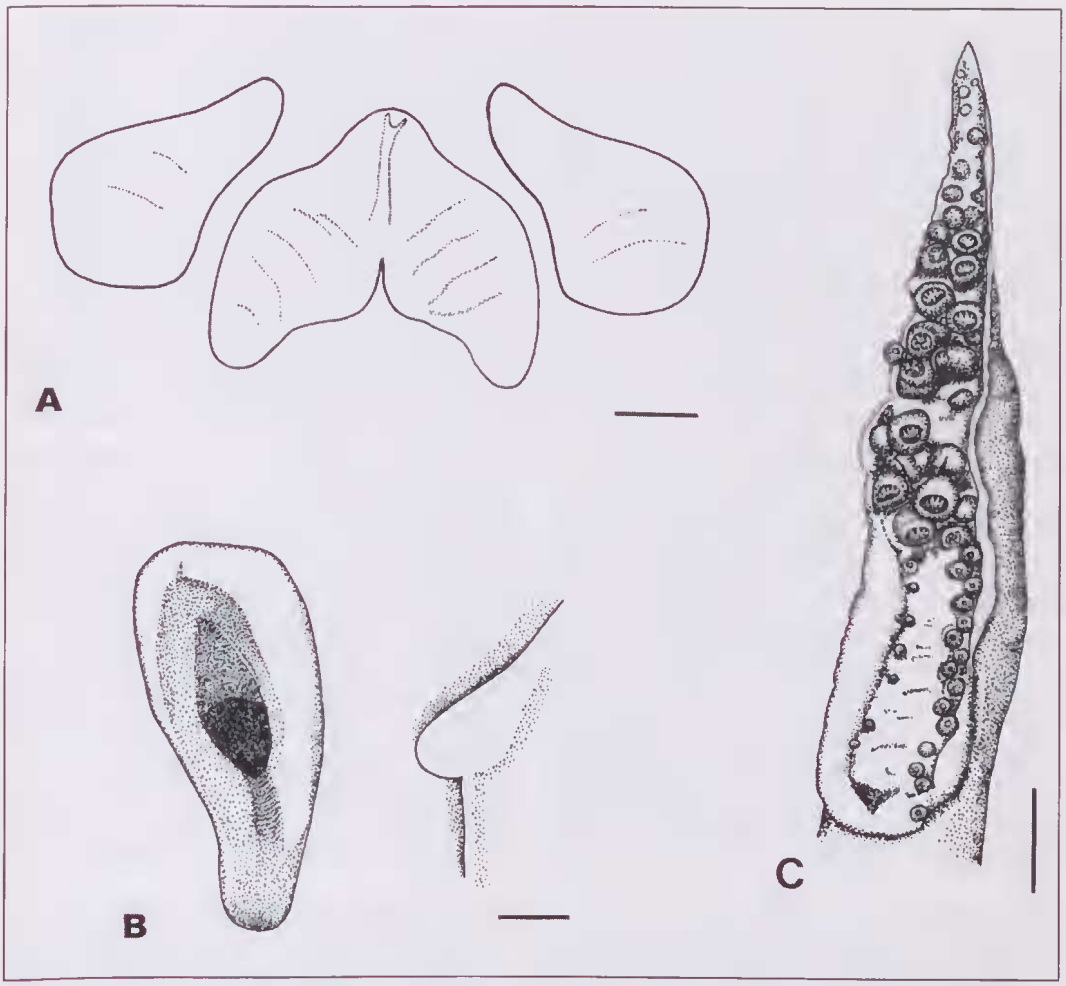

Fig. 13. *Sepiella weberi*: **A**, funnel organ, female, MV F65575, 47.1 mm ML, scale bar 2 mm; **B**, funnel locking cartilage (left), and mantle locking cartilage (right), male syntype, ZMA Moll.2.39.002, 59.7 mm ML, scale bar 1 mm; **C**, hectocotylus, male syntype, ZMA Moll.2.39.002, scale bar 2 mm.

LoL/StZ(%) males 52.9–71.4–90.0 (SD, 26.3), females 50.0–67.3–100.0 (SD, 19.3), loculus extending posteriorly as narrow margin on each side of striated zone. Sulcus extending entire length of cuttlebone; shallow, narrow; flanked by rounded ribs. Last loculus with shallow median indentation, not very pronounced. Anterior striae inverted U-shape, slightly wavy. Limbs of inner cone short, extending anteriorly to junction of striated zone and posterior termination of last loculus. Inner cone limbs uniform width, narrow; thickened slightly; not raised to form ledge posteriorly (Fig. 19D). Outer cone chitinous, spatulate, expanded; narrow anteriorly, broadening posteriorly; posterio-lateral wall without, or with very weak indentation in both sexes; limbs expanded, extending posteriorly beyond inner cone, recurved ventrally (Fig. 19C–D).

Papillae absent. Colour (alcohol preserved specimens): head and arms purplish brown; dorsal mantle pale, peppered with scattered purple-black chromatophores (Fig. 12A); paired dorsal eye spots absent. Fins pigmented; with five to six oval orange-pink spots at base of fins in both sexes, spots slightly larger, and more prominent in males. Ventral pigment present, pale (Fig. 12B).

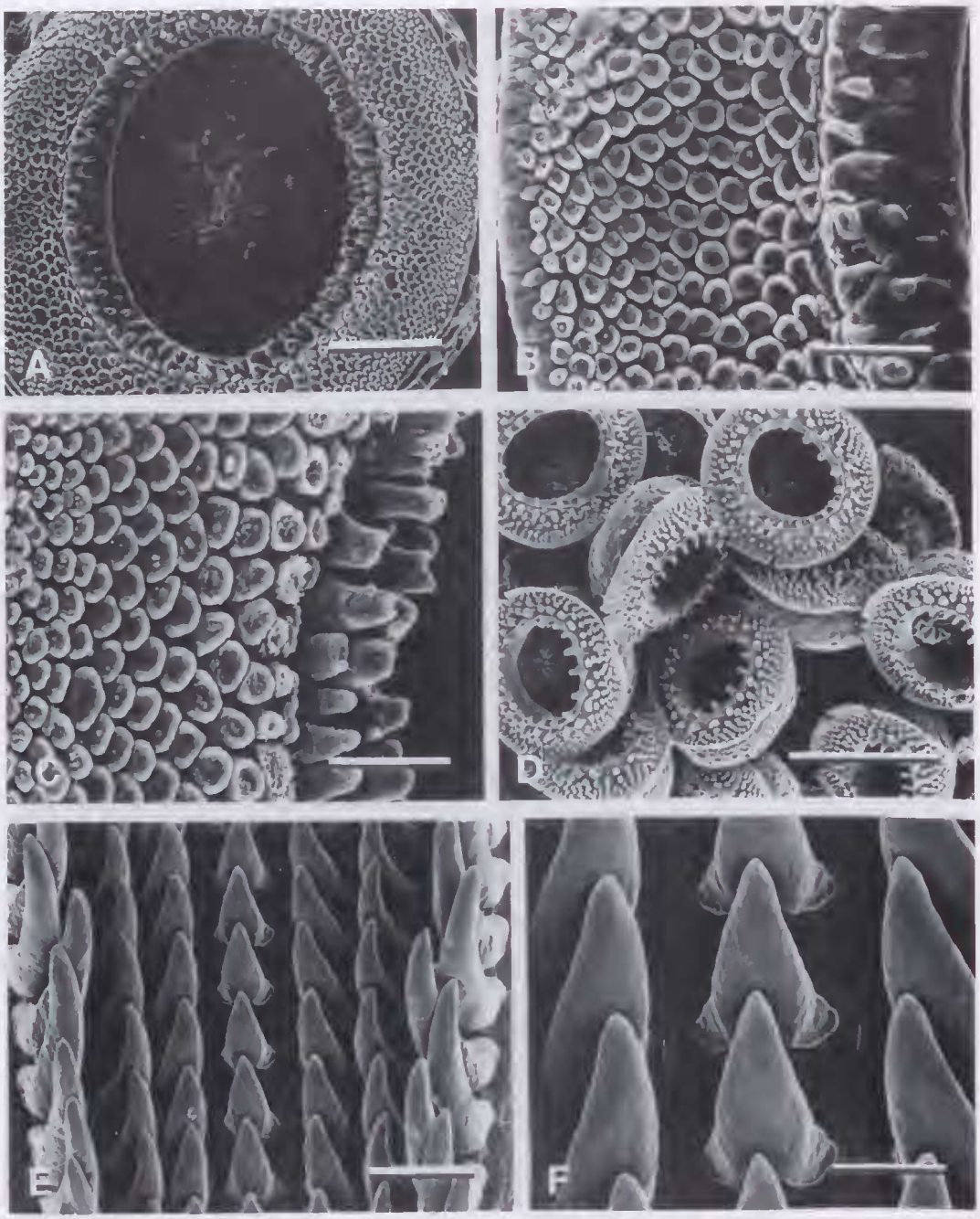

Fig. 14. *Sepiella weberi*: **A**, sucker rim, arm 2, female, MV F71713, 49.7 mm ML, scale bar 100 μm; **B**, enlargement of arm sucker rim, same specimen, scale bar 10 μm; **C**, enlargement of inner side of arm sucker rim, same specimen, scale bar 10 μm; **D**, club suckers, female, MV F65575, 54.3 mm ML, scale bar 200 μm; **E**, radula, female, MV F71713, 49.7 mm ML, scale bar 200 μm; **F**, enlargement of first lateral (left) and rhachidian teeth, same specimen, scale bar 100 μm.

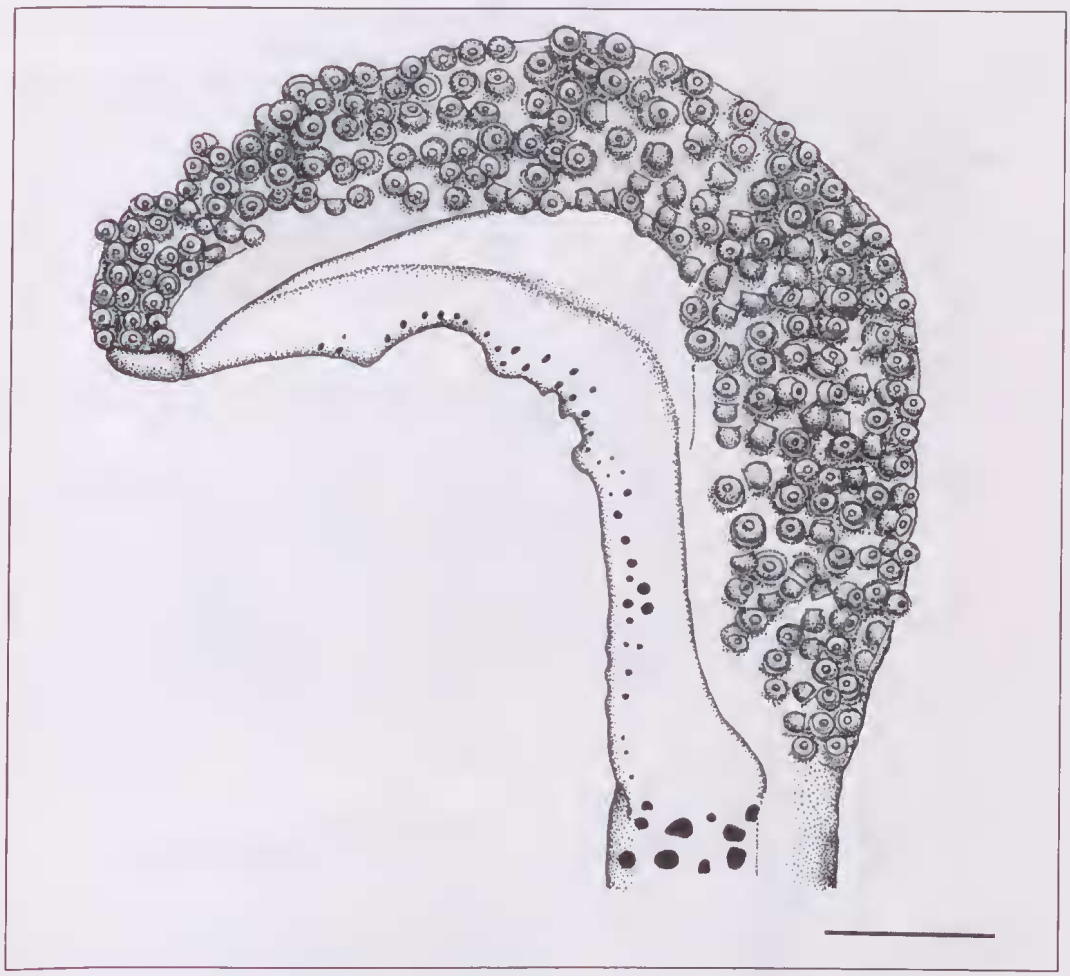

Fig. 15. *Sepiella weberi*: tentacular club, female, MV F65575, 50.0 mm ML, scale bar 2 mm.

Distribution. Indonesia (Timor – Soemba) 8°35'S 126°00'E – 10°S 119°56'E to northwestern Australia 12°39'S 127°03'E – 19°35'S 117°14'E (Fig. 10). Depth range surface to 88 m (see Remarks).

Remarks. The female syntype from Soemba, Indonesia (ZMA Moll.3.39.001) differs slightly from all remaining specimens in having the swimming keel slightly shorter, rather than equal to the carpus in length. It does not differ in other respects to the other material examined. Differences between *Sepiella weberi* and *S. mangkangunga* sp. nov. are given in the Remarks section of *S. mangkangunga* sp. nov. above. Table 6 shows some characters which differ between all nominal *Sepiella* species. In contrast to *S. weberi*, in all other *Sepiella* species, the ventral side of the cuttlebone is strongly convex medially. In other characters, *S. weberi* is very similar to *S. cyanea*, differing primarily in the shape of the cuttlebone. The posterior end of the striated zone is more acuminate in *S. cyanea* than in *S. weberi* (Adam and Rees 1966). The shape of the bone differs also from *S. ocellata*. The bone of the latter species is narrower, and uniform in width throughout its length, while in *S. weberi* the bone is wider in the posterior half. The bone in *S. inermis* is much wider than that of *S. weberi*, and distinctly oval in outline, rather than oblong. The sulcus is deeper and much more well defined in *S. inermis* than in *S. weberi*, and *S. inermis* has

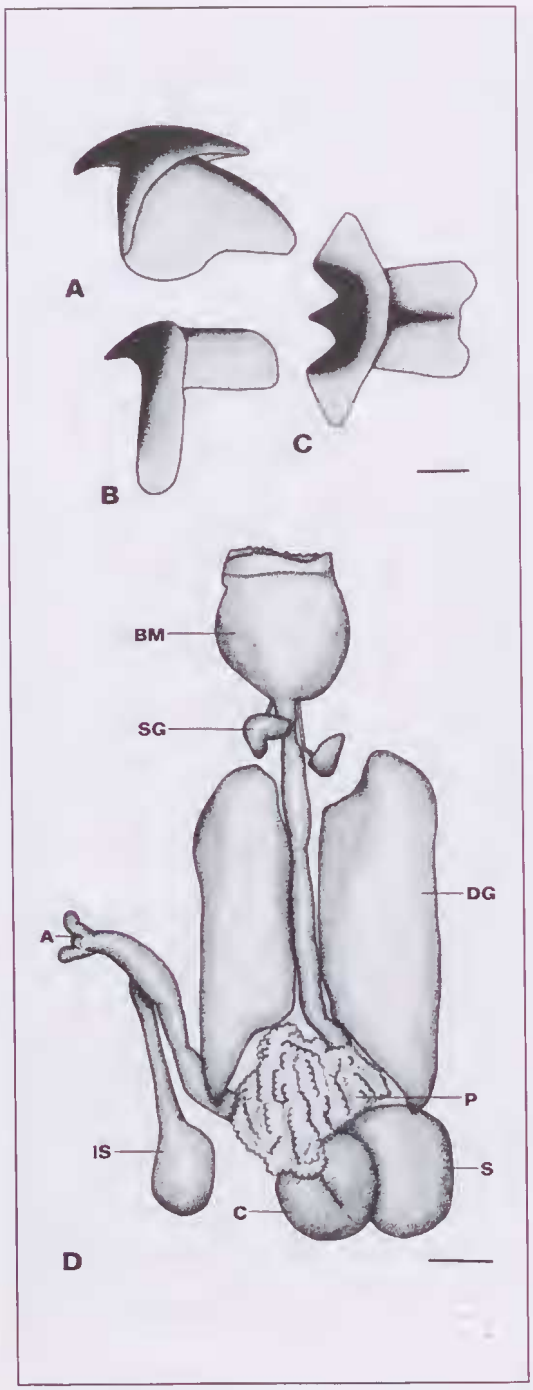

Fig. 16. *Sepiella weberi*: **A**, upper beak, lateral view; **B**, lower beak, lateral view; **C**, lower beak, ventral view (A-C, male, MV F65579, 44.5 mm ML, scale bar 2 mm); **D**, digestive tract, dorsal view, female, MV F65575, 53.2 mm ML, scale bar 2 mm, abbreviations as in Figure 6D.

12–20, while *S. weberi* has 7–10 club suckers in transverse rows.

The Australian *S. weberi* were all collected between 88 and 77 m depth, while the syntypes from Indonesia were found in shallower water. The female syntype was collected at 18 m. The male syntype was caught at the surface at night following attraction to lamp light, suggesting there may be a nocturnal migration into shallower waters.

Key to the species of *Sepiella* found in Australian waters

Dorsal mantle with ovoid spots at base of each fin. Tentacular club with 12-15 suckers in transverse rows; swimming keel shorter than carpus. Cuttlebone strongly convex in lateral view ..... *S. mangkangunga* sp. nov.

Dorsal mantle without ovoid spots at base of each fin. Tentacular club with 7–10 suckers in transverse rows; swimming keel terminates at level of carpus. Cuttlebone not strongly convex in lateral view ..... *S. weberi* Adam

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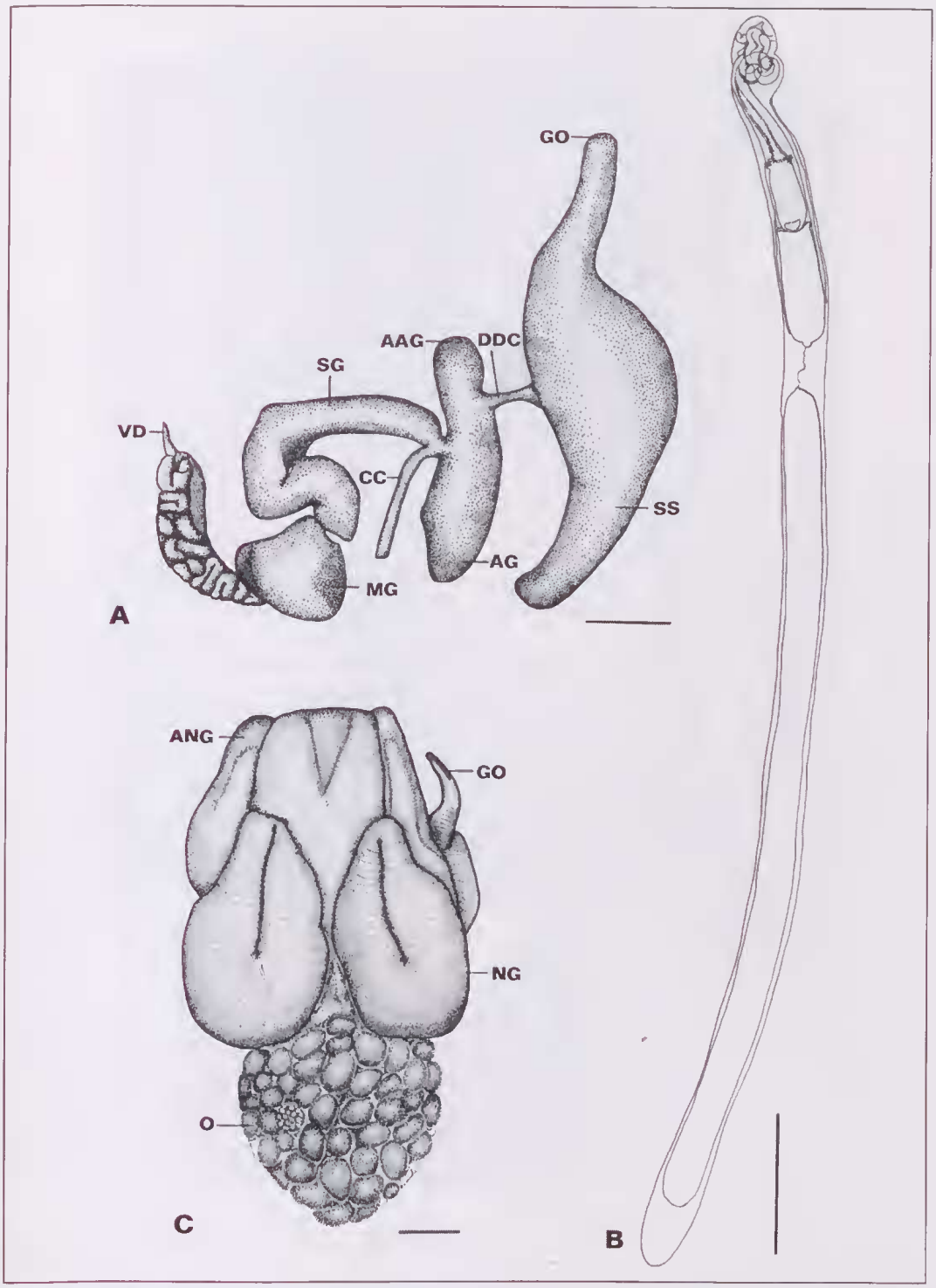

Fig. 17. *Sepiella weberi:* **A**, male genital duct MV F65579, 44.5 mm ML, scale bar 1 mm, abbreviations as in figure 7A; **B**, spermatophore, male, MV F65571, 56.8 mm ML, seale bar 0.5 mm; **C**, female genital duct MV F65575, 53.2 mm ML, scale bar 3 mm, abbreviations as in Figure 7C.

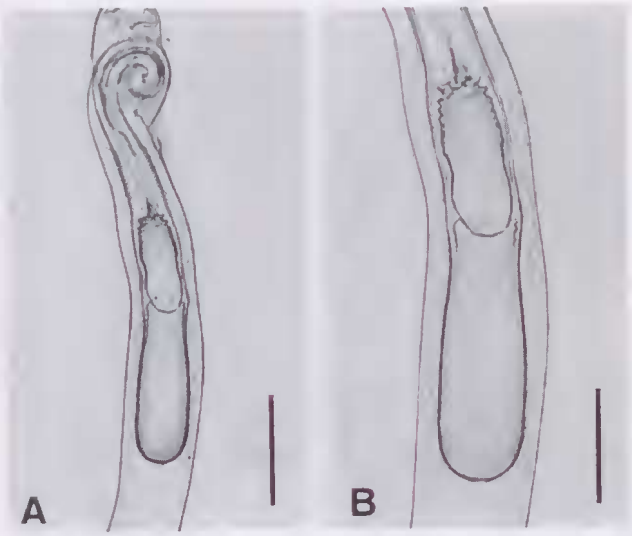

Fig. 18. *Sepiella weberi*: **A**, spermatophore, oral end, male, MV F65571, 56.8 mm ML, scale bar 0.3 mm; **B**, enlargement of ejaculatory apparatus, same specimen, scale bar 0.1 mm.

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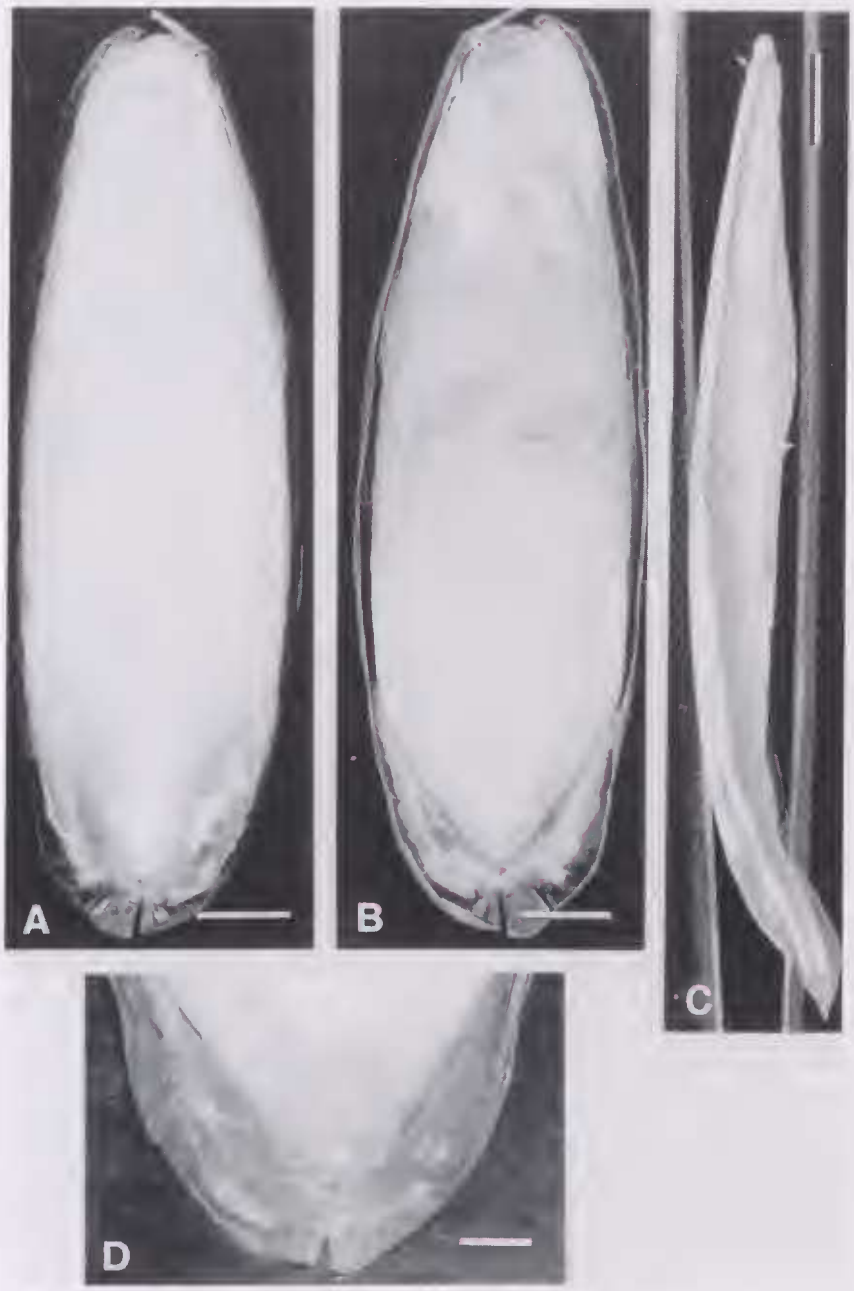

Fig. 19. *Sepiella weberi*: **A**, cuttlebone dorsal view, female, MV F65575, 47.1 mm ML, scale bar 5 mm; **B**, cuttlebone ventral view, same specimen; **C**, cuttlebone lateral view, male, MV F65571, 56.8 mm ML, scale bar 5 mm; **D**, posterior end of cuttlebone, ventral view, female, MV F65575, 47.1 mm ML, scale bar 2 mm.

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